VARIATIONS IN FEEDING BEHAVIOR, SURVIVAL AND DAMAGE OF BIOTYPES B AND E OF SCHIZAPHIS GRAMINUM (RONDANI) ON THREE WHEAT GENOTYPES

By

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VARIATIONS IN FEEDING BEHAVIOR, SURVIVAL, AND DAMAGE OF BIOTYPES B AND E OF SCHIZAPHIS GRAMINUM (RONDANI) ON THREE WHEAT GENOTYPES

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TABLE OF CONTENTS

Chapter		Page
I.	INTRODUCTION	1
II.	LITERATURE REVIEW	4
	A. General Biology of The Insect	4
	1. Life Cycle	4
	2. Biotypes	4
	3. Genetics of Greenbugs	6
	B. Feeding	7
	1. Mouthparts	7
	2. The Feeding Mechanism and Site	7
	3. Feeding Behavior	8
	C. Damage	9
	D. Host Plant Resistance	10
	1. Historic Review	10
	2. Searching for Greenbug Resistance	11
	3. Insect Adaptation to Resistant Genotypes	11
	4. Biochemistry of Resistance	12
III.	MATERIALS AND METHODS	14
	A. Feeding Monitor	15
	B. Survival	18
	1. Greenbug Growth and Honeydew Collection	18
	2. Honeydew Extraction and Measurement	19
	3. Measurements on Aphids	20
	C. Damage - Chlorophyll Extraction and Measurement	20
	D. Data Analysis	21

Chapter Page

IV. RESULTS 22

A. Feeding Behavior 22

1. Baseline. 22
2. Probes. 22
3. Salivation. 28
4. X-waves 29
5. Phloem Ingestion. 37
6. Progression of Behavioral Events in Time. . . . 37
a. Biotype E 37
b. Biotype B 43

B. Survival 43

1. Growth. 43
2. Honeydew Production 44

C. Damage 55

V. DISCUSSION. 63

VI. SUMMARY AND CONCLUSIONS 70

REFERENCES CITED 72

LIST OF TABLES

Table		Page
I.	Mean Duration of Behavioral Activities (Baseline, Salivation, Phloem Ingestion, and Non Phloem Ingestion) for 720 Minutes By Two Greenbug Biotypes Feeding on Three Wheat Genotypes.	23
II.	Mean Number of Probes, and X-Waves During 720 Minutes of Monitoring Greenbug Biotypes B and E on Three Wheat Genotypes	29
III.	Mean Time to First X-Wave, and Committed Phloem Ingestion During 720 Minutes of Monitoring Greenbug Biotypes B and E on Three Wheat Genotypes.	34
IV.	Feeding Behavior per Four Hour Intervals of Monitoring Greenbug Biotypes B and E on Three Wheat Genotypes.	42
V.	Mean Greenbug Numbers, Live Weights, Dry Weights, and Live Weight per Insect (Weights Are in Milligrams) of Greenbug Biotype B and E Fed on Three Wheat Genotypes for 10 days	45
VI.	Mean Greenbug Numbers, Total Honeydew, Honeydew per Greenbug, and Honeydew per Greenbug per Dry Weight (HD/GB/DW) Produced by Biotype B and E Feeding on Three Wheat Genotypes for 10 days	50
VII.	Total Chlorophyll Measurements (MG/G of Fresh Weight) of Infested and Uninfested Leaves, and Percent Chlorophyll Reduction Due to Biotypes B and E Feeding on Three Wheat Genotypes	58

LIST OF FIGURES

Figure — Page

1. Mean Baseline Duration Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105 25

2. Mean Number of Probes Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105 27

3. Mean Salivation Duration Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105 31

4. Mean Numbers of X-Waves Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105 33

5. Time (in minutes) it Takes for the Greenbug to Make its First X-wave as Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105 36

6. Mean Phloem Ingestion Duration Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105 39

7. Time (in minutes) it Takes for the Greenbug to Start Its Committed Phloem Ingestion (lasting more than 15 minutes) as Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105. 41

8. Mean Greenbug Biotypes B and E Numbers Produced During 10 Days of Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105. 47

9. Average Live Weight (in milligrams) per Greenbug of Biotype B and E Feed on Three Wheat Genotypes for 10 Days TAM 105L = Largo x TAM 105. 49

10. Total Honeydew Produced (in milligrams) by Greenbug Biotypes B and E Fed on Three Wheat Genotypes for 10 Days TAM 105L = Largo x TAM 105. 52

11. Average Honeydew Produced (in milligrams) per Greenbug Biotypes B and E Fed on Three Wheat Genotypes for 10 Days TAML = Largo x TAM 105. 54

Figure Page

12. Average Honeydew Produced Per Greenbug and Per Unit Dry Weight for 10 Days of Feeding on Three Wheat Genotypes TAM 105L = Largo x TAM 105 57

13. Total Leaf Chlorophyll Content (in mg/g of leaf per weight) of Three Wheat Genotypes Before (check uninfested) and After 10 Days of Greenbugs Biotype B and E Feeding TAM 105L = Largo x TAM 105 60

14. Percent Chlorophyll Reduction Due to Greenbug Biotypes B and E Feeding on Three Wheat Genotypes for 10 Days TAM 105L = Largo x TAM 105 62

CHAPTER I

INTRODUCTION

The greenbug, Schizaphis graminum (Rondani), is one of the most important pests of cereals (wheat, barley, sorghum and oats). Damage due to this insect has been reported most frequently in the United States, Italy, Hungary, Russia, and South Africa (Wadley, 1931). The Commonwealth Institute of Entomology (1963) indicated that the insect was present in all continents; at least ten countries in Africa, 13 in Asia, nine in Europe and five in South America plus Mexico, Canada, Australia, and the Pacific Islands have the greenbug.

The pest was reported to have been in the United States since 1882 (Webster and Philips, 1912). The 1907 and 1951 outbreaks each caused about $50 million loss in Oklahoma, Kansas and Texas (Walton, 1921; Dahms et al. 1955). In 1976, the greenbug infestation in Oklahoma cost about $80 million for control and production loss (Starks and Burton, 1977).

Greenbugs introduce their stylets into plant tissue to withdraw sap, and in this feeding process saliva is injected into the plant system. This saliva is thought to contain compounds that are harmful to the plant and greatly increases the potential damage (Chatters and Schlehuber, 1951). The ability of aphids to penetrate the plant tissues varies with the plant, but the more successful the penetration the more damage is likely to occur. Therefore, it is desirable to understand how

the greenbug feeds and causes damage in order to successfully develop effective resistant varieties.

The objectives of my research were:

1. To compare the feeding behavior of greenbug biotypes B and E on selected resistant and susceptible wheat genotypes. It has been shown that aphid feeding behavior could be influenced by many factors including the host genotype. Thus, if greenbugs are exposed to different hosts, there could be feeding behaviorial differences. I would expect greenbugs to exhibit more phloem ingestion on the susceptible than on resistant hosts. Conversely, the insects should show less activity (more baseline), more attempts to penetrate the leaf tissues (probes), more time spent salivating, and more attempts to reach the phloem to feed (X-waves) on resistant plants than on susceptible ones.

To my knowledge no one has used the feeding monitor to study the greenbug feeding behavior of biotypes B and E on TAM 105, TAM 107, and Largo x TAM 105 wheat genotypes. Therefore, my study should provide additional information on greenbug biotypes B and E and on how the three wheat genotypes affect these insects.

2. To study the survival of the greenbug biotypes B and E on resistant and susceptible wheat genotypes. It has been demonstrated that greenbugs reproduce less on resistant than on susceptible plants. Thus, there should be a difference in the total number of nymphs produced, their relative weights, and honeydew production on the above biotype/genotype combinations. The resistant genotypes should result in lower greenbug survival rates than the susceptible.

3. To characterize damage due to greenbug biotypes B and E on selected wheat genotypes. Biotype E damages TAM 105 and TAM 107,

however, it is not known to cause significant damage to wheat lines containing the 'Largo' gene for greenbug resistance. A cross between Largo and TAM 105, (with four backcrosses to TAM 105) and selected for greenbug resistance after backcrossings, is expected to behave like a resistant genotype to biotype E, when compared to TAM 105 and TAM 107. TAM 107 contains the broken resistance, 'Amigo' gene, to biotype E and was expected to respond in a similar way as TAM 105 does to biotype E.

The 'Amigo' gene for greenbug resistance present in TAM 107 provides resistance to biotype B, recently shown to have broken the 'Largo' gene for resistance to biotype E (Webster et al., 1986). Thus, damage due to biotype B on TAM 107 was expected to be significantly lower than that on TAM 105 and Largo x TAM 105 genotype.

Overall, damage due to greenbug biotype E on the Largo x TAM 105 genotype should be similar to that due to biotype B on TAM 107 since these entries are resistant to the respective greenbug biotypes. Susceptible (TAM 105) and broken resistances to the respective biotypes were expected to show comparable damage.

CHAPTER II

LITERATURE REVIEW

A. General Biology of the Insect

1. Life Cycle

The type of reproduction usually found in the greenbug is parthenogenesis. The reproductive period can extend from 12 to 53 days (Abebe, 1983; Webster and Phillips, 1912) depending on the season. A wingless female greenbug may produce one to eight nymphs per day (Walton, 1921). On the average, the nymphal stage lasts seven days during which the nymph passes through four instars before reaching the adult stage. Nymphal growth depends on temperature, and as indicated by Kirkland et al. (1981) the threshold for nymphal growth is 5°C and the optimum is 30°C. Within this range, the relationship between temperature and nymphal growth is linear and under field conditions, a stadium lasts approximately 28-30 hours.

2. Biotypes

Greenbugs can produce 20-25 generations a year (Webster and Phillips, 1912). The production of such large numbers of generations is possible because of parthenogenesis. In this type of reproduction, aphids can produce populations of similar genetic background which may be adapted to a particular cultivar or species of plant or to a particular

environment (Dixon, 1985). Such populations are often referred to as "races" or "biotypes"; terminologies used to describe aphids' ability to adapt to their hosts. Plant resistant biotypes were noted by Painter (1930) after comparing damage to wheat caused by different populations of Hessian fly, Mayetiola destructor (Say). He observed that the Hessian flies from eastern Kansas was more virulent than the ones from western Kansas.

Scientists have attempted to define the "biotype" concept in several ways. Hatchett and Gallun (1970) proposed a definition based on genetic relationship between the host (wheat) and the pest (Hessian fly), "For every major gene for resistance in the host species, there is a corresponding matching gene for virulence in the parasite species". Their definition which implied gene matching was an extension of Flor's (1955) gene for gene concept regarding rust on flax. Eastop (1973) added that "aphids which can feed on a normally pest resistant plant may be referred to as a biotype". Within aphid populations, a biotype may also be considered as those individuals differing from others by characters other than morphology including parasitic ability (Gallun and Khush, 1980). This may be a questionable statement, because investigations by Inayatullah et al. (1985) have shown that morphological differences could exist among greenbug biotypes. These authors identified a greenbug biotype which damages sorghum and breaks the 'Largo' source of resistance in wheat. This was described as biotype B even though the form observed in 1958 and reported by Wood (1961) has not been reported in Oklahoma for several years. Moreover, the original B was not a pest of sorghum. I will use biotype B in this thesis even though another designation such as "Largo breaking biotype" might be more descriptive.

Biotype C was reported in 1968 by Harvey and Hackerott (1969) as damaging grain sorghum. Biotype D was reported by Teetes et al. (1975) as able to survive disulfoton treatment. Biotype E was first reported by Porter et al. (1982) as breaking the 'Amigo' resistance source.

Some investigators have questioned the biotype idea. Claridge and Hollander (1983) suggested that further genetic studies are needed in order to give more value to the concept. For these authors, the concept as of today is a broad one based on virulence and with ignorance of insect and host genetics.

3. Genetics of Greenbugs

The genetics of greenbugs is not clearly known; also the genetics of biotypes has not been thoroughly investigated. With the objective of providing additional information on greenbug biotypes, Mayo and Starks (1972) used a chromosome staining technique to compare chromosomes of three known biotypes (A, B, and C). Comparisons were based on chromosome size, number and general morphology. Embryos from aphids were used and ten chromosome sets were measured at each meiotic stage to obtain their lengths. They found that all three biotypes possessed eight chromosomes which could be grouped into one large pair, one small pair, and four chromosomes intermediate in size and not distinctly paired. A Chi-square test showed that biotype B differed from A in all chromosomal comparisons but was similar to C. Apparently, biotype formation involves some genetic changes in the greenbugs. This suggests the possibility of gene matching between the insect and the host, and perhaps the ability of the insect to better feed on the host.

B. Feeding

1. Mouthparts

The greenbug has piercing-sucking mouthparts that allow it to extract plant sap for food. Saxena and Chada (1971) described the insect's mouthparts using electron microscopic techniques by which they were able to distinguish two mandibular and two maxillary stylets. The mandibular stylets are innervated. Each mandible has a central duct through which a nerve passes, and this canal also contributes to the flexibility of the stylets. There are three to four longitudinal grooves common to the maxillae of which the second grooves (largest) of right and left maxillae form the food canal (0.12 micron in diameter). The salivary canal is formed by the third groove of the right maxilla. The four stylets have four protractor and retractor muscles, also four rotator muscles for the mandibles. A sphincter muscle at the conical tip of the labium surrounds the stylets.

2. The Feeding Mechanism and Site

Feeding is a dual process in which aphids extract sap via the food canal and inject saliva into the plant via the salivary canal. Stylet penetration into the plant tissues is facilitated by contraction of the protractor muscles and downward movement of head. The maxillae can slide up and down against each other so that the greenbug can change the course of the stylets inside the plant tissue. In the feeding process, the aphid may actively suck sap by means of the pharyngeal pump (Pollard, 1973). Chatters and Schlehuber (1951) pointed out that the major greenbug feeding site in wheat and barley was the phloem, and that the

saliva injected was the cause of damage. Saxena and Chada (1971) showed that biotype B fed preferentially in mesophyll parenchyma when susceptible 'Rogers' barley was used as a host. They also indicated that both intercellular and intracellular penetration occurred. Pennington (1985) studied probing behavior and damage by biotype C and E on barley. Her conclusion was that penetration is generally intercellular in the case of biotype E, but occasionally intracellular in biotype C. She also demonstrated penetration of the xylem by greenbugs.

3. Feeding Behavior

The first histological study on greenbug feeding behavior on wheat and barley was done by Chatters and Schlehuber (1951). Penetration was compared on 11 cultivars of wheat and barley. Greenbug feeding may be divided in two major sequences: 1) host selection and 2) feeding behavior. The host selection is comprised of three steps: host location, movement toward host, and contact. As Beck and Schoonhoven (1980) pointed out, host selection is a series of behavioral responses associated with internal drives to find ovipositional and feeding sites. Pollard (1973) indicated that light reflected from the host (wave length), color of host and odor were some of the factors that affect host finding. Upon contact with a potential host, the aphid exhibits a feeding behavior which is also a sequential phenomenon comprising four events usually referred to as probing, salivation, penetration and ingestion.

McLean and Kinsey (1967) were able to trace the tissue region that an aphid contacts during the above behavioral sequences. Their study was conducted using the pea aphid, Acyrthosiphon pisum (Harris) and a feeding

monitor that they had developed earlier (McLean and Kinsey, 1964). They recorded waveforms associated with each feeding sequence and designated those as "S" salivation, "I" ingestion. They recognized the "X" and "Y" wave forms but they were not able to give their characterization. They also found that in 484 aphids monitored, the events occurred most often in the following sequences: 1) salivation, then ingestion; 2) salivation, X-wave - Y-wave - ingestion; and 3) salivation - X-wave - ingestion. All the waveforms were measures of the voltage changes as the aphid fed. Salivation corresponded to high voltage peaks in a rapid succession whereas ingestion corresponded to a flat pattern. Another study (McLean and Kinsey, 1968) was conducted to determine variations in salivation and ingestion of A. pisum on host (broadbean, Vicia faba L.) and nonhost (lettuce, Lactuca sativa L.) plants. They found that the first probing resulted in ingestion (70% of aphids) regardless of the host, but there was a significant difference in probing, salivation and ingestion between host and nonhost as aphids stayed longer on the plant.

C. Damage

In general, damage due to greenbugs has been described in terms of reduction in plant growth (stunting), destruction of chlorophyll (chlorosis), and plant death if damage was severe. Ortman (1957) studied damage of the greenbug on wheat varieties ('Pawnee', 'Ponca', 'Bison', and 'Dickinson'). He infested plants with different numbers of greenbugs. The progenies were allowed to feed for seven days in one experiment and from two to 10 days in another. His results showed that leaf length, dry weight, and chlorophyll were adversely affected by the

greenbug feeding. Furthermore, he added that there was a reduction in root weight which may cause several adverse plant conditions (lodging, less water absorption, and translocation of nutrients).

Many researchers have tried to explain the cause of the symptoms which occur with greenbug feeding. The authors above hypothesized that damage may be due to several factors such as interference of injected toxins with some metabolic and translocation processes in the plant. Chatters and Schlehuber (1951) had attributed symptoms to the salivary injection rather than food uptake, but Ortman (1957) thought that the food uptake by the insect was enough to cause reduction in roots. Gerloff and Ortman (1971) found a reduction in the rate of photosynthesis following greenbug feeding. Al-Mousawi et al. (1983) compared greenbug damage at the cellular level on a susceptible wheat variety (TAM 101) and a resistant one (TAM 101 x Amigo). They found that there was extensive damage to the mesophyll cells in the susceptible as opposed to the resistant, and that saliva produced was responsible. They postulated that this saliva could be dissipated or adsorbed by resistant tissues and fewer symptoms were noted in these plants.

D. Host Plant Resistance

1. Historic Review

A historic review of host plant resistance was given by Ortman and Peters (1980). They indicated that the earliest documentation on resistance was by Havens who in 1792 reported the wheat variety 'Underhill' to be resistant to Hessian fly. Since this early report, plant resistance has become an important discipline in applied

entomology. It is commonly agreed that varietal resistance is one of the most economical methods to control insects such as the greenbug.

2. Searching For Greenbug Resistance

Dahms et al. (1955) tested many varieties of wheat, barley, rye and oats for their response to greenbugs. Varieties that survived greenbug attack (so presumed resistant) were tested for preference, antibiosis and tolerance. They also studied inheritance of resistance in barley. Among the wheat varieties, some durums showed tolerance and one, Dickinson No. 485, CI 3707, was considered resistant.

Painter and Peters (1956) tested 2141 strains of wheat with 'Pawnee' as a susceptible check and 'Dickinson' as a resistant check. They infested six to seven day old seedlings with greenbugs, then graded the plants based on a 1 to 5 damage scale (1 = no damage, - 5 = death). The grading started at about two weeks after infestation. Another similar study was conducted by Wood and Curtis (1967) in which pure-line selections of susceptible 'Ponca' and resistant 'Dickinson' wheats were artificially infested with greenbugs and yields were measured for four seasons. Resistant selections produced higher yield than susceptible selections.

3. Insect Adaptation to Resistant Genotypes

The appearance of biotypes that overcome previous resistance has been an intriguing problem to entomologists. For instance, resistance in 'Dickinson' has been overcome by biotype B (Wood 1961). A more recent example is that of 'Amigo' derived from 'Gaucho' triticale, which was previously resistant to greenbug biotype C (Wood et al., 1974). It was

overcome by biotype E (Porter et al., 1982). 'Largo' was reported as greenbug resistant by Joppa et al. (1980), but was overcome by the new B biotype (Inayatullah et al., 1985). Thus, efforts to breed resistant genotypes have been challenged by greenbugs. It becomes necessary to consider what could be potential sources for resistance and to know the genetics of resistance so that resistant gene transfer could be more effective and that more durable resistance be obtained. The 'Largo'gene has shown high resistance to biotype E in addition to its already known resistance to biotype C (Joppa et al., 1980). Hollenhorst and Joppa (1983) found the 'Largo' gene to be located in the 7D chromosome whereas the 'Amigo' gene is located in chromosome 1A.

4. Biochemistry of Resistance

There have been several different approaches to the biochemistry of greenbug resistance. Maxwell and Painter (1962) measured variations in free auxin content of extracts of the S. graminum and A. pisum fed on resistant or susceptible wheat and alfalfa hosts. The following results were obtained: a) In susceptible 'Reno' barley, 3-indole-acetic acid and 3-indolebutyric acid were present in significant amounts; b) In susceptible 'Pawnee' wheat, 3-indoleacetic acid was present; but c) These auxins were not found in resistant 'Dictoo' barley or 'Dickinson' wheat. The absence of auxins (non significant amounts) in the honeydew of aphids feeding on resistant plants was believed to be due to 1) inability of the greenbug to remove auxins from resistant plants, 2) only small amounts were removed, or 3) auxins were removed but not in significant concentration in the aphids bodies.

Host plant resistance is often believed to be due to the presence of

secondary metabolites. In wheat such phenolic compounds as DIMBOA (Corcuera et al., 1982) are feeding deterrents to S. graminum. Pennington (1985) showed that penetration results in more silica deposition in barley tissues and that resistant barley 'Will' to biotype E contained more phenolic compounds. Also, she noted that the levels of these compounds changed following aphid feeding, indicating a possible relation between the compounds and aphid feeding.

Pectinases are important enzymes in aphid feeding. Campbell and Dryer (1985) suggested that alterration of intercellular pectins or other chemicals in sorghum could reduce the effectiveness of greenbug pectinases, thus providing another way of obtaining resistance to aphids.

CHAPTER III

MATERIALS AND METHODS

The experiments were conducted in the Controlled Environment Research Lab (CERL) at Oklahoma State University. Temperature in the feeding monitoring room recorded by a hygrothermograph was 26° ± 4°C, and relative humidity was 34 ± 5%, the photoperiod was 12 hrs light and 12 hrs dark.

Seeds of three wheat genotypes, TAM 105, TAM 107, and Largo x TAM 105[4] were obtained from Dr. Owen Merkle, Wheat Breeder, USDA, Plant Sciences Laboratory, Stillwater, Oklahoma.

Greenbug biotype E had been in culture for several months from specimens collected on sorghum in West Lafayette, Indiana. Biotype B individuals were obtained from C. Inayatullah's colony (Ullah 1985).

TAM 105 wheat is a release from Texas A & M University (Porter et al., 1980), and was selected from a composite bulk made up originally of F_2 seed from crosses and backcrosses of several short experimental wheats to 'Scout'. It is susceptible to biotypes C and E.

TAM 107 wheat is a release from Texas A & M University. It has the 'Amigo' gene for resistance to biotype C, but this resistance was broken by biotype E. This genotype was a selection from Amigo X TAM 105 backcrossed four times to TAM 105 and selected for greenbug resistance after each backcross.

Largo x TAM 105 is a resistance source to biotype E but broken by

biotype B. 'Largo' was produced by a cross between Triticum turgidum (L.), and Triticum tauschii (Coss.), and is an hexaploid and an amphiploid of the two wheats. Dr. Owen Merkle has been backcrossing several agronomically desirable lines with 'Largo' including the Largo x TAM 105 we used.

TAM 105 was expected to be susceptible to biotype B as well as E. TAM 107 contained the 'Amigo' gene which was broken by biotype E but this gene was expected to confer resistance to biotype B. The cross of Largo by TAM 105 was expected to be resistant to biotype E but not to biotype B. Therefore, I had two susceptible, two resistant and two "broken resistance" biotype/genotype combinations to evaluate.

Seeds of the above entries were placed in petri dishes for germination. Two or three days later, the germinated seeds were transferred into preweighed pots and filled to 280g with air-dried sandy loam soil. The pots were watered to 330g (field capacity) with 25% Hoagland's solution every other day. The plants were kept in a growth chamber in which fluorescent and incandescent lights were combined for optimum growth. The photoperiod was 14 hrs light and 10 hrs dark, and the temperature was 20°C $\pm$ 0.5°C. After three weeks, plants with a fully formed third leaf were chosen for the experiments.

A. Feeding Monitor

Electronic feeding monitors which have been modified several times from original equipment of McLean and Kinsey (1964, 1967) were used. The monitors used in this experiment were a modification of Brown and Holbrock (1976), and built by Kendow Technologies, Perry, Oklahoma. Included was a 25 Hertz oscillator connected to the test plant, a 25

Hertz tuned amplifier rectifier that received signals from the test aphid, and a chart recorder. The oscillator converted direct current (supplied by the batteries) into alternating current, and the amplifier amplified the signal to readable levels. The strip chart recorder was operated at 0.5 cm per minute to record the changes in voltage. A plexiglass stand held an attached pot into which the test pots and plants were placed and a vertical, flat plastic piece from which the lead wire was suspended. This stand had two plugs and wires - one connected to the plant by the pot soil and one connected to a copper rod to which 10 micron diameter and 3 cm long gold wire was glued.

This system was less subject to interference because the tuned amplifier could amplify the desired signals while the undesired background signals were reduced to the minimum. Compared to Brown and Holbrock's system, this feeding monitor used two 9-volt batteries which gave off less electrical interference. Other monitors using transformed wall current (60 Hz) require much more electrical screening.

To prepare the aphid for monitoring, a drop of silver glue was placed on the slide and the tip of a 3 cm long, 10 micron diameter wire was dipped in the drop until a ball was formed. Subsequently the greenbug dorsum was pressed to the ball of silver glue and thereby attached to the wire. The leaf used for monitoring was flattened and taped on the plexiglass stand. The insect was placed on the leaf as soon as possible, and the corresponding amplifier turned on.

When the conductive saliva from greenbug mouthparts contacted the plant tissues, an electric circuit was completed. There was a direct current flowing from the two 9-volt batteries into the oscillator where it is changed to a 25 Hz oscillating current, passed into the pot soil,

to the plant, to the aphid and to the gold wire. From the gold wire, the current flowed to the "monitor" input, then filtered into the amplifier. The signal was amplified and rectified before the changes in voltages were transmitted on to the strip chart recorder where they were recorded. The amplitude of the current was adjusted by manipulating the gain knob. Six feeding monitors were used per monitoring session. Combinations of plant/greenbug biotype were selected at random within the block and were randomly assigned to monitors. Greenbug feeding was monitored for 12 hours. The runs usually began at 9:00am and therefore were not completed until after the lights went off at 7:00pm.

Overall there were eight blocks with six plants per block. There were six replacements making a total of 54 aphids monitored on 54 different seedlings.

The chart records were read to identify the feeding behavior codes and corresponding times. The adopted feeding behavior codes (BC) were identified as follows:

BC.0: Baseline: describes the period when aphid's mouthparts are not in fluid contact with the plant tissue, and no current is flowing in the system; in other words, baseline is when the greenbug is not feeding.

BC.1: Probe: describes penetration of the plant epidermal tissues by the aphid's stylets. It is seen as a sharp voltage spike followed by a sharp drop. This is thought to represent sheath material being released (highly conductive) and its subsequent hardening (less conductive).

BC.2: Salivation: describes active stylet movement within the plant. It is seen as a saw-shaped fluctuation in voltage. The fluctuation may correspond to successive secretion of watery saliva and sheath saliva

accompanied by hardening of the sheath saliva. The result is an irregular waveform of intermediate amplitude.

BC.3: Describes an unknown behavior. It is seen as a low voltage wave with only very slight amplitude fluctuations. There are speculations that this may be due to closed sheath at tissues just below the stylets of the feeding aphid, it may be a resting behavior, but with the stylets in the tissues (Ryan, personal communication).

BC.4: X-Wave: Is seen as an H-shaped wave of 40 seconds average duration. It always precedes phloem ingestion, but does not necessarily end up in phloem ingestion.

BC.5: Phloem ingestion: It is seen as a relatively smooth tracing with very slight, changes in voltage. The phloem is considered the preferred feeding site for the greenbug.

BC.6: Non-phloem ingestion: The wave pattern is different from all of the above. The stylets may be in mesophyll or xylem cells. In this study, I have combined BC.3 and BC.6 and will refer to all this activity as non-phloem ingestion.

B. Survival

1. Greenbug Growth and Honeydew Collection

After each replicate was monitored (usually the next day) part of the third leaf on the plant was caged for honeydew collection. The caged leaf portion was also used to study greenbug survival and feeding damage. Using the same leaf should facilitate correlation of the feeding monitoring data to the amount of honeydew produced and greenbug biomass increase.

Cylindric and transparent plexiglass cages about three cm high and

three cm in diameter with small nails in the bottom to hold them on stands of rectangular styrofoam covered with soft foam were used for this experiment. The piece of styrofoam on each stand was covered with aluminum foil so that no honeydew was lost. The stand was inserted in each pot adjacent to the plant. Each leaf was then laid flat on the styrofoam and two cages were placed over it. Subsequently, two adult greenbugs of the appropriate biotype were placed in each cage which was then closed with a fitted foam rubber stopper. The adult aphids were removed the next day, and six nymphs per cage were allowed to grow and reproduce on the host for a period of 10 days. At the end of the 10th day, the cages and foils were removed and cleaned of exuviae before they were put in tagged paper bags. All the aphids on each leaf were brushed off into transparent 120ml plastic specimen jars which were also tagged. Each caged portion of the leaf was excised and placed in a tagged plastic bag. Thus, feeding behavior, greenbug counts and weights, honeydew production and chlorophyll content, were taken on the same plant/biotype combination. Only four replicates were used in the greenbug growth, fecundity, honeydew, and chlorophyll content studies.

2. Honeydew Extraction and Measurement

A 500 ml beaker was filled to 125 ml with deionized water and placed on an electric plate. Small foil cups were tagged and weighed (W_1). About 5 ml (at a time) of hot water was then poured into a preweighed cup, also placed on the hot plate to keep the water and cup warm. The washing of the foil and the cages was done repeatedly using the water from the cup (5ml), then at the end additional hot water (5-15ml) was sucked to rinse the foil and the cages. The cup, with the honeydew in

solution, was taken off the hot plate and set aside. The process was repeated until all cages were cleaned. All the cups, containing honeydew and water mixture, were placed in an oven at 70°C to evaporate the water. After 24 hours they were removed from the oven and their weight (W_2) taken. The difference between the two weights ($W_2 - W_1$) was the amount of honeydew produced.

3. Measurements on Aphids

The aphids were counted and weighed immediately for live weight. Then they were oven dried at 70°C for at least 24 hours to obtain their dry weights. This allowed the estimation of aphid biomass, live weight per greenbug, and dry weight per greenbug, honeydew per weight greenbug dry weight and honeydew weight per greenbug live weight.

C. Damage-Chlorophyll Extraction and Measurement

The chlorophyll extraction method was modified from techniques described by MacKinney (1941) and Arnon (1949). Weights (and areas) of leaf samples were determined and the leaf sample kept in the freezer until immediately prior to chlorophyll analysis. Each leaf sample was placed in a mortar with 0.1g of $CaCO_3$ and "pinch" of acid washed sand. The leaf was cut with scissors into smaller pieces and ground with a pestle until completely macerated. Eighty-five percent acetone was used to clean the mortar and the pestle. Rinsing and stirring was continued until all chlorophyll had been extracted. The solute was then filtered through a Whatman #2 filtering paper into a volumetric flask. The filter paper was rinsed repeatedly to remove any remaining chlorophyll. The volume was brought up to 25 ml with 85% acetone, then the flask was

capped and kept in a closed box (to prevent light penetration). The process was repeated for all the leaf samples.

Absorbance readings were taken at 645 nanometers and 663 nanometers. These values were inserted in the following formula to obtain total chlorphyll readings:

$$\text{Total chlorophyll (mg/g of leaf)} = \frac{(20.2 \times A645 + 8.02 \times A663)V}{W.}$$

A_{645} = absorbance at 645mM

A_{663} = absorbance at 663 mM

V = Total volume of volumetric cap in Cm^3 here 25 ml.

W = Leaf weight in g

D. Data Analysis

Data input was on a remote terminal to an IBM 3081K system. Data were analyzed with analysis of variance (SAS Institute, 1982, 119-137) and tests of genotype/biotype combinations were compared using the "t" test (SAS Institute, 1982, 217-221). Inherent in the experimental design, which included the two wheat genotypes whose resistance had been overcome or "broken" by the respective biotypes, was a great potential for biotype/genotype interaction. My choice was to consider differences in genotypes and biotypes only if the interaction for the respective characteristics was not significant at $P < 0.10$ and to use the two tailed "t" test to compare the genotype by biotype combinations for all characteristics investigated. I am aware that there are more rigorous tests for mean comparisons, but considering the potential sources of variability of genotypes, biotypes and interpretation of insect behavior, the consistent application of the "t" test appeared to be a reasonable choice.

CHAPTER IV

RESULTS

A. Feeding Behavior

1. Baseline

There was a significant difference ($P \leq 0.05$) in baseline time between the resistant and susceptible genotypes to biotype E (Table I, Fig. 1); biotype E on Largo X TAM 105 stayed inactive longer than it did on TAM 105 or TAM 107. Baseline was considered a weak criterion for behavior since greenbugs readily probe many plants and baseline time was also an accumulation of time after all withdrawals from less desirable host leaves. The genotype/biotype combination, Largo x TAM 105 with biotype E, caused the greatest difficulty in overall monitoring and three of eight recordings were repeated due to broken tethers, aphids wandering off plants or uninterpretable recordings.

2. Probes

Biotype B probed significantly more often on TAM 107 than on TAM 105 ($P < 0.10$) (Table II, Fig. 2) and Largo x TAM 105 was intermediate between these two.

When I examined probing by biotype E on these genotypes, I could see that this greenbug probed significantly more often on the resistant Largo x TAM 105 genotype compared to the susceptible TAM 105 ($P < 0.10$) (Table

TABLE I

MEAN DURATION OF BEHAVIORAL ACTIVITIES (BASELINE, SALIVATION, PHLOEM INGESTION, AND NON PHLOEM INGESTION) FOR 720 MINUTES BY TWO GREENBUG BIOTYPES FEEDING ON THREE WHEAT GENOTYPES

Wheat Genotypes	Greenbug Biotype	TIME IN MINUTES			
		Baseline	Salivation	Phloem Ingestion	Non-Phloem Ingestion
TAM 105	E	15.9a[1]	116a	553a[2]	29a[2]
TAM 105	B	15.3a	187ab	499a	13a
TAM 107	E	25.3a	165ab	454ab	71a
TAM 107	B	26.0a	273b	344bc	66a
Largo x TAM 105	E	66.8b	210ab	229c	205b
Largo x TAM 105	B	16.6a	218ab	451ab	25a
TAM 105	Both	15.6x	151x	526x	21x
TAM 107	Both	25.7xy	219x	399y	68x
Largo x TAM 105	Both	41.7y	214x	340y	115x
All	E	36.0e	164e	412e	101e
All	B	19.3e	226f	431e	35f

[1] Values with the same letters are not significantly different (t test, $P \leq 0.05$).

[2] Values with the same letters are not significantly different (t test, $P \leq 0.10$). Comparisons were restricted to biotype/genotype combinations, or genotypes and biotypes within each column.

Figure 1. Mean Baseline Duration Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105

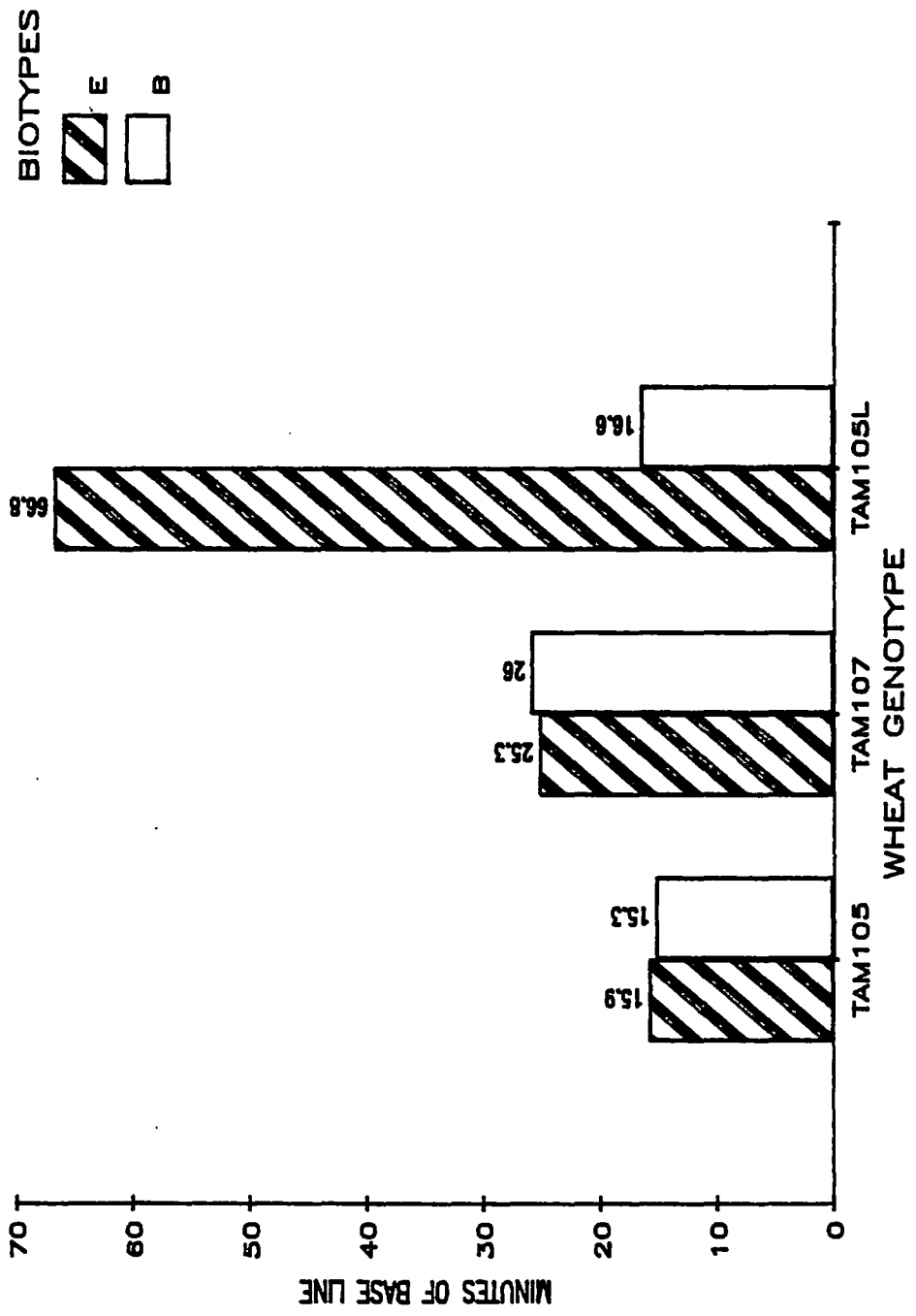
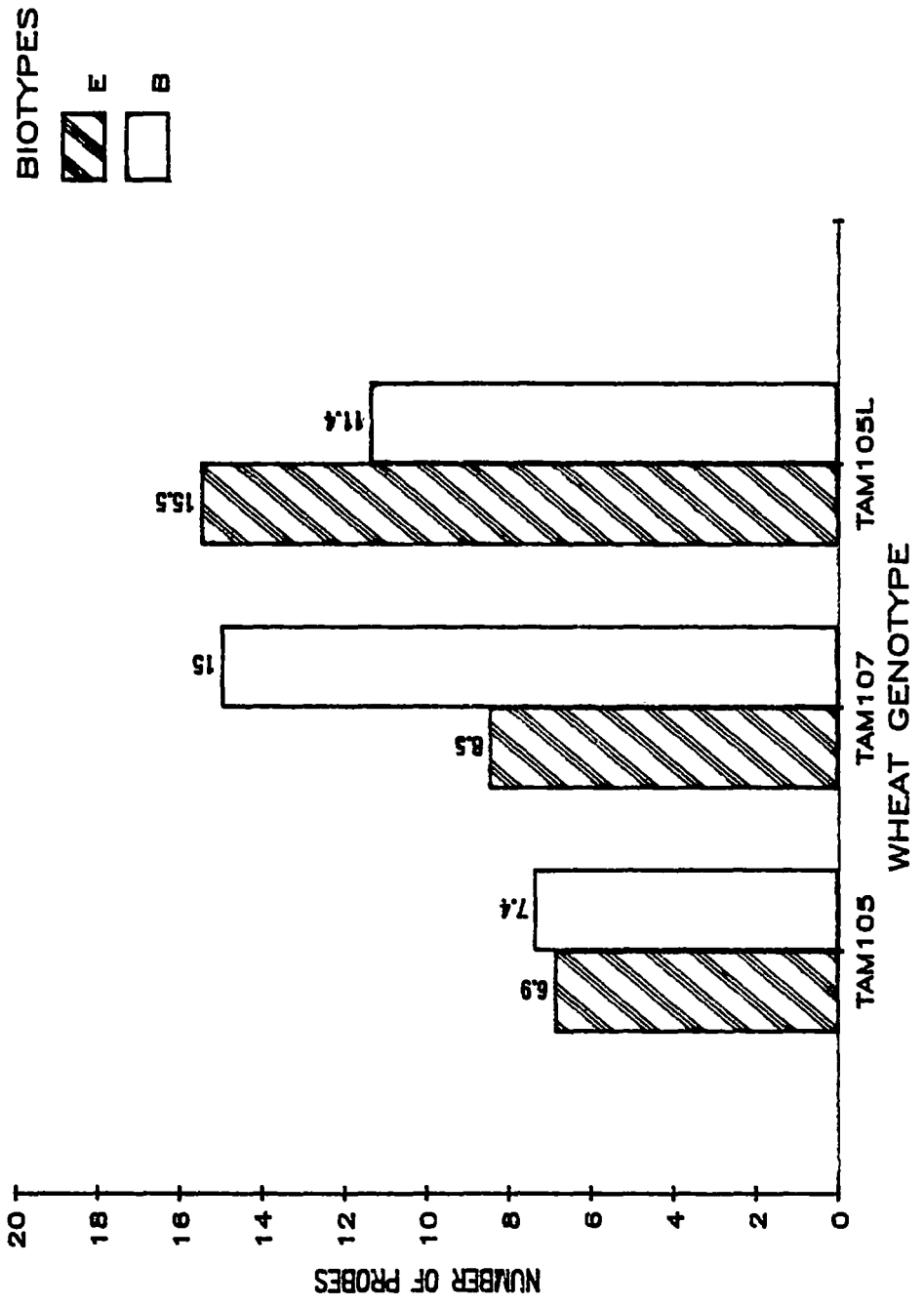

BIOTYPES
E
B
MINUTES OF BASE LINE
0
10
20
30
40
50
60
70
15.9
15.3
25.3
26
66.8
16.6
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

Figure 2. Mean Number of Probes Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105


BIOTYPES
E
B
NUMBER OF PROBES
0
2
4
6
8
10
12
14
16
18
20
6.9
7.4
8.5
15
15.5
11.4
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

II, Fig. 2). TAM 107, a broken resistance to E behaved more like a susceptible and was not statistically different from the other two genotype combinations.

The overall statistical test among genotypes showed that there was a difference between susceptible (TAM 105) and the respective resistant genotypes. The broken resistances were variable and not statistically different from either the resistant or susceptible host genotype.

3. Salivation

The total salivation duration, was higher on resistant genotypes for both biotypes. Broken resistances were intermediate between susceptible and resistant. Biotype B salivated longer over all genotypes than biotype E ($P \leq 0.05$) Table I, Fig. 3). This pattern was consistant when compared at the progression in salivation in 4-hour intervals.

4. X-waves

Biotype E made fewer X-waves on TAM 107 than biotype B made on TAM-107 and than both biotypes made on Largo x TAM 105 ($P \leq 0.10$) (Table II, Fig. 4). I could not show a difference for biotype B among the respective genotypes. However, biotype B made more X-waves than biotype E on all genotypes. When I looked at the time it took for the insects to start an X-wave, I could see that biotype E took longer on Largo x TAM-105 than on any other genotype and that biotype B did not show any differences based on host genotypes (Table III, Fig. 5). The two biotypes on the respective broken resistant genotypes behaved differently; B made more X-waves than E did.

TABLE II

MEAN NUMBER OF PROBES, AND X-WAVES DURING 720 MINUTES OF MONITORING GREENBUG BIOTYPES B AND E ON THREE WHEAT GENOTYPES

Wheat Genotype	Greenbug Biotype	Mean Number of Probes	Mean Number of X-Waves
TAM 105	E	6.9a[1]	3.0ab
TAM 105	B	7.4a	5.3ab
TAM 107	E	8.5ab	2.8a
TAM 107	B	15.0b	6.0b
Largo x TAM 105	E	15.5b	6.3b
Largo x TAM 105	B	11.4ab	6.6b
TAM 105	Both	7.1x	4.1x
TAM 107	Both	11.8xy	4.4x
Largo x TAM 105	Both	13.4y	5.5x
All	E	10.3e	4.0e
All	B	11.3e	6.0f

[1] Values with same letter are not significantly different ($P < 0.10$). Comparisons were restricted to biotype/genotype combinations, or genotypes and biotypes within each column.

Figure 3. Mean Salivation Duration Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105

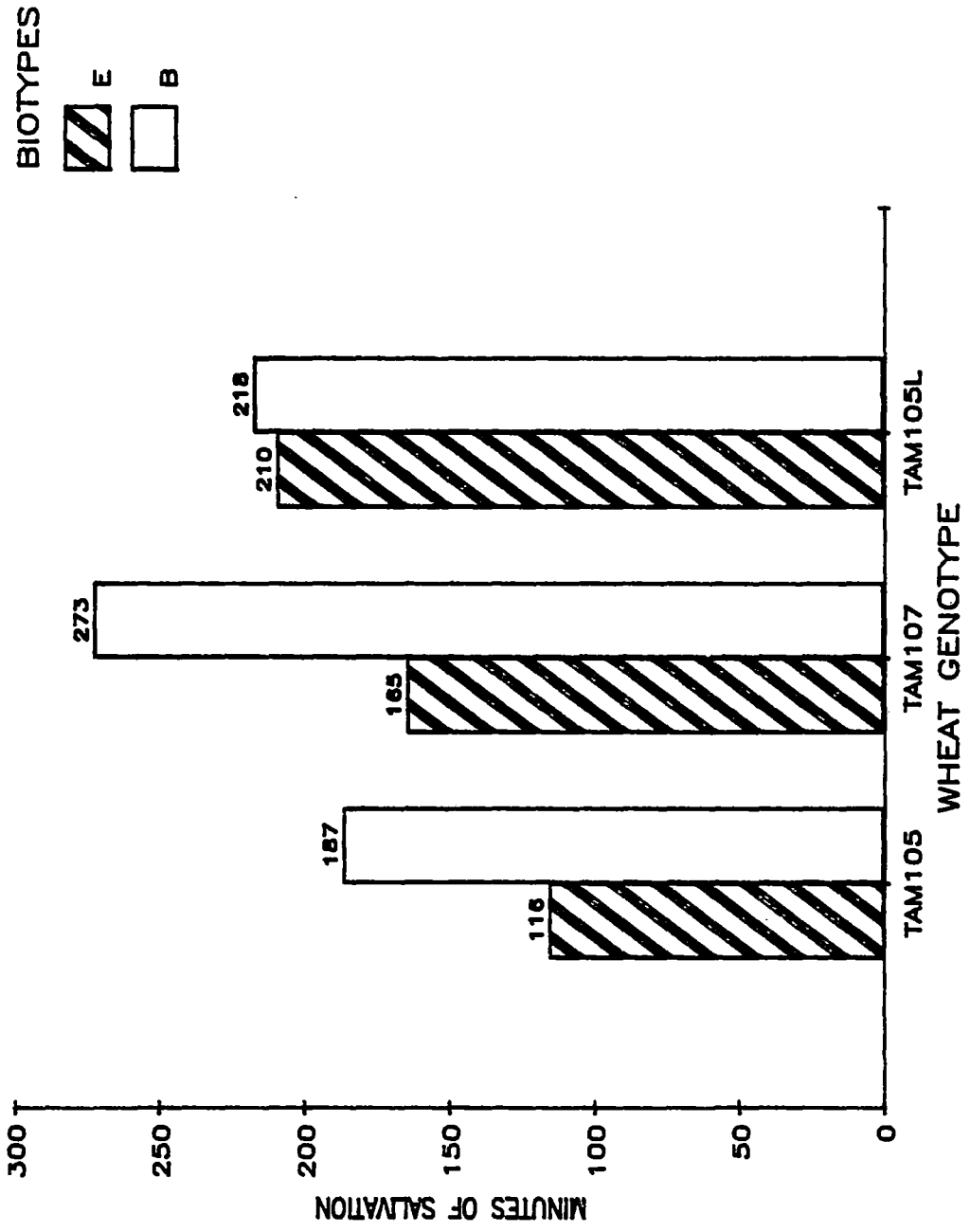

BIOTYPES
E
B
MINUTES OF SALIVATION
300
250
200
150
100
50
0
116
187
165
273
210
218
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

Figure 4. Mean Numbers of X-Waves Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105

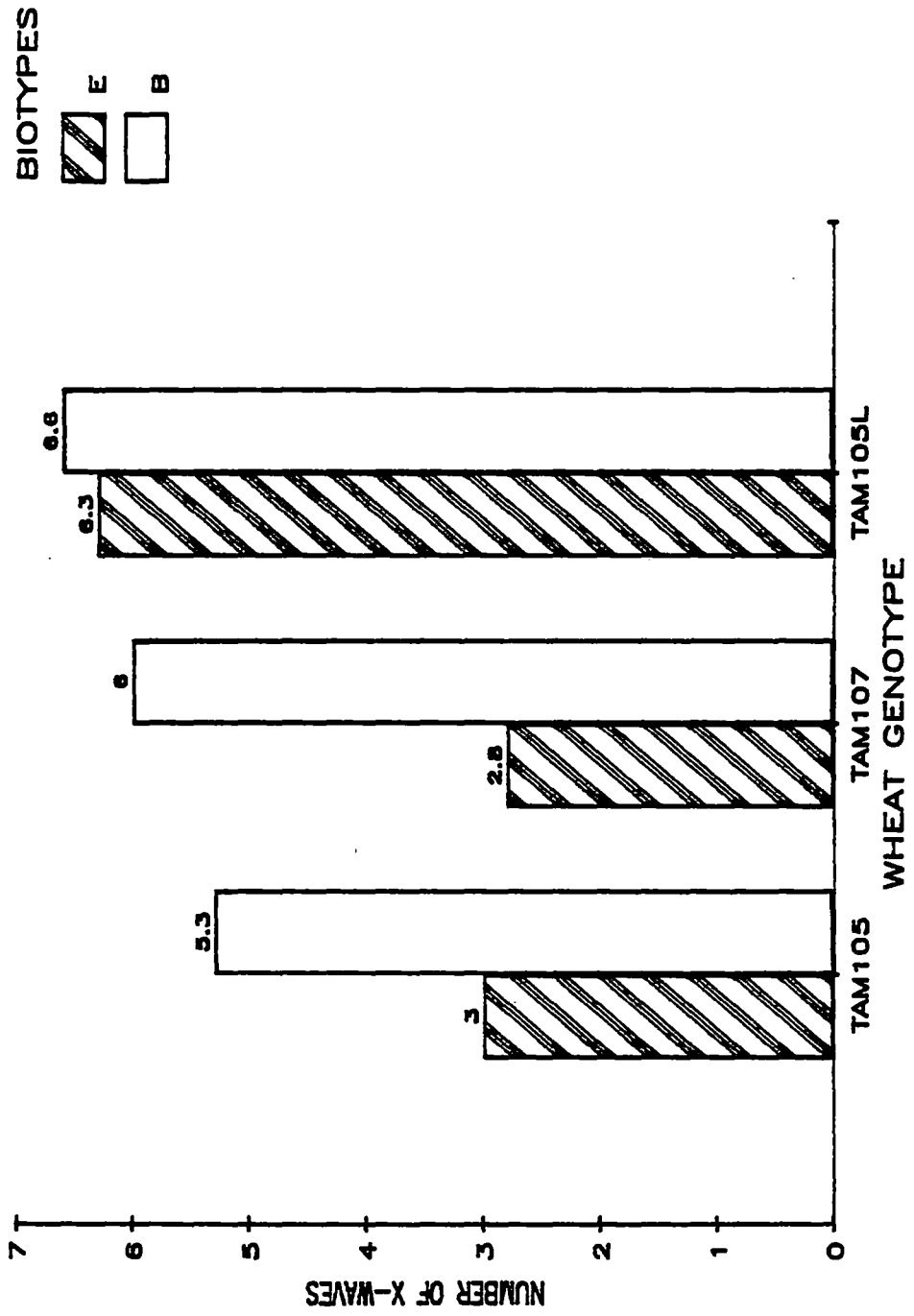

BIOTYPES
E
B
NUMBER OF X-WAVES
0
1
2
3
4
5
6
7
3
5.3
2.8
6
6.3
6.6
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

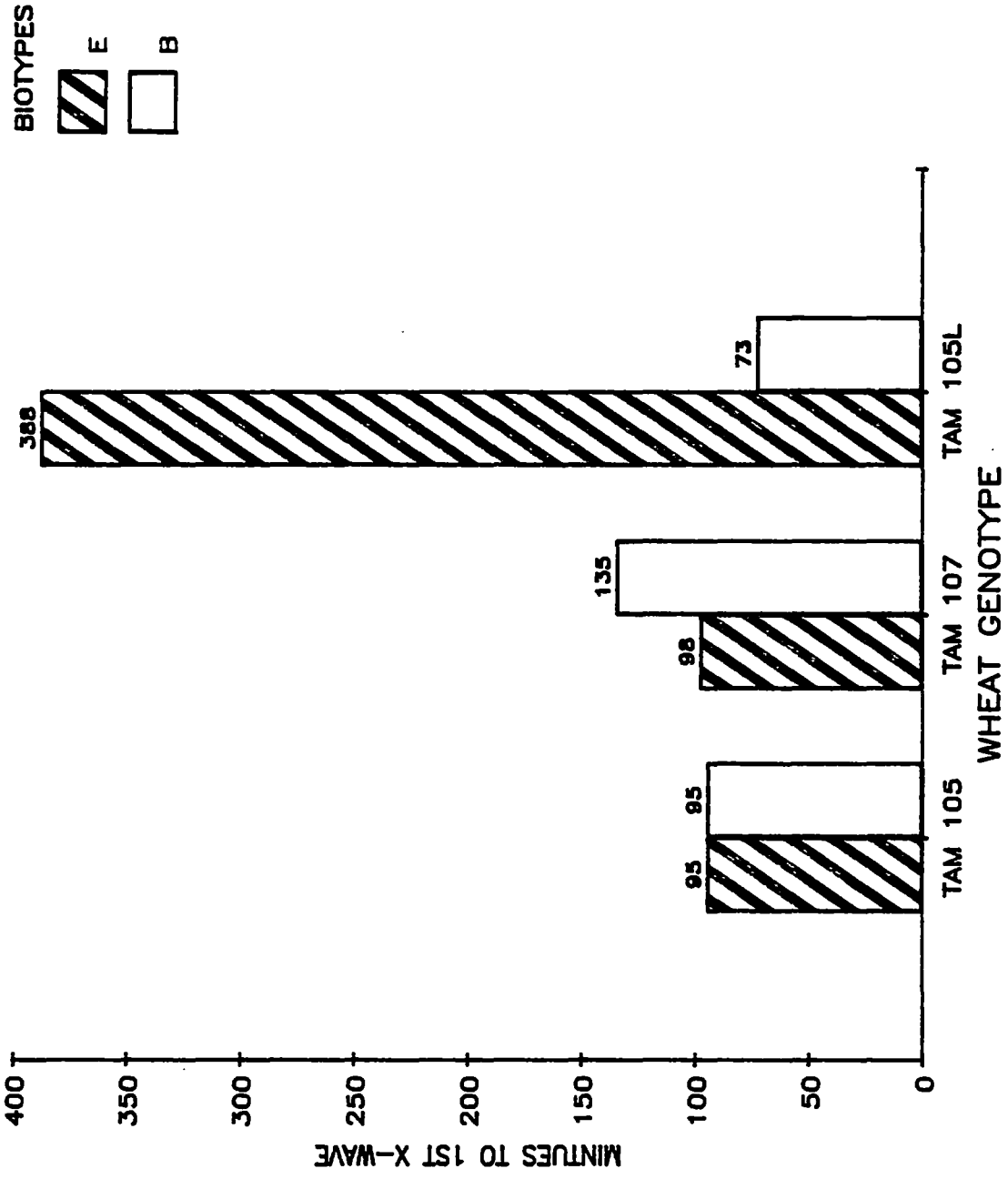
TABLE III

MEAN TIME TO FIRST X-WAVE, AND COMMITTED PHLOEM INGESTION DURING 720 MINUTES OF MONITORING GREENBUG BIOTYPES B AND E ON THREE WHEAT GENOTYPES

Wheat Genotype	Greenbug Biotype	Minutes to 1st X-Wave	Minutes to First Committed Phl. Ing.
TAM 105	E	95a [1]	128a
TAM 105	B	95a	197a
TAM 107	E	98a	168a
TAM 107	B	135a	195a
Largo x TAM 105	E	388b	434b
Largo x TAM 105	B	73a	183a

[1] Values with same letters are not significantly different ($P < 0.10$).

Figure 5. Time (in minutes) it Takes for the Greenbug to Make its First X-wave as Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105


BIOTYPES
E
B
MINTUES TO 1ST X-WAVE
400
350
300
250
200
150
100
50
0
388
73
135
98
95
95
TAM 105
TAM 107
TAM 105L
WHEAT GENOTYPE

5. Phloem Ingestion

For both biotype B and E, phloem ingestion was longer on the susceptible compared to resistant genotypes. The respective broken resistant genotypes were intermediate (Table I, Fig. 6). The largest difference existed between 'Largo' containing genotypes and TAM 105 when exposed to biotype E. It took significantly ($P \leq 0.05$) longer for biotype E to achieve first committed (15 minutes or more continued behavior) phloem ingestion on Largo x TAM 105 than on TAM 105 (Table III, Fig. 7). The pattern was the same as that seen in the number of X-waves.

6. Progression of Behaviorial Events in Time

a. Biotype E During the first four hours of monitoring (Table IV), this biotype showed slightly more salivation time, and extensively more phloem ingestion on TAM 105 than on Largo X TAM 105. The two forms of non-phloem ingestion were seen at high frequencies and extended time in the Largo x TAM 105 genotype. Largo x TAM 105 had the highest baseline duration, probes, and non-phloem ingestion during the first four hours. In the broken resistance, TAM 107, the phloem ingestion was intermediate; this was also true for the non-phloem ingestion.

During the next four hours, baseline, probes, salivation, and non-phloem ingestion were reduced, but more phloem ingestion occurred on TAM-105 compared to Largo x TAM 105. Again, biotype E on Largo x TAM 105 had the highest salivation duration and X-wave frequency. The broken resistance was different from the susceptible TAM 105, and showed reduced non-phloem ingestion and salivation, but more phloem ingestion than the 'Largo' containing genotype.

By the third 4-hour period biotype E on TAM 105 continued phloem

Figure 6. Mean Phloem Ingestion Duration Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105

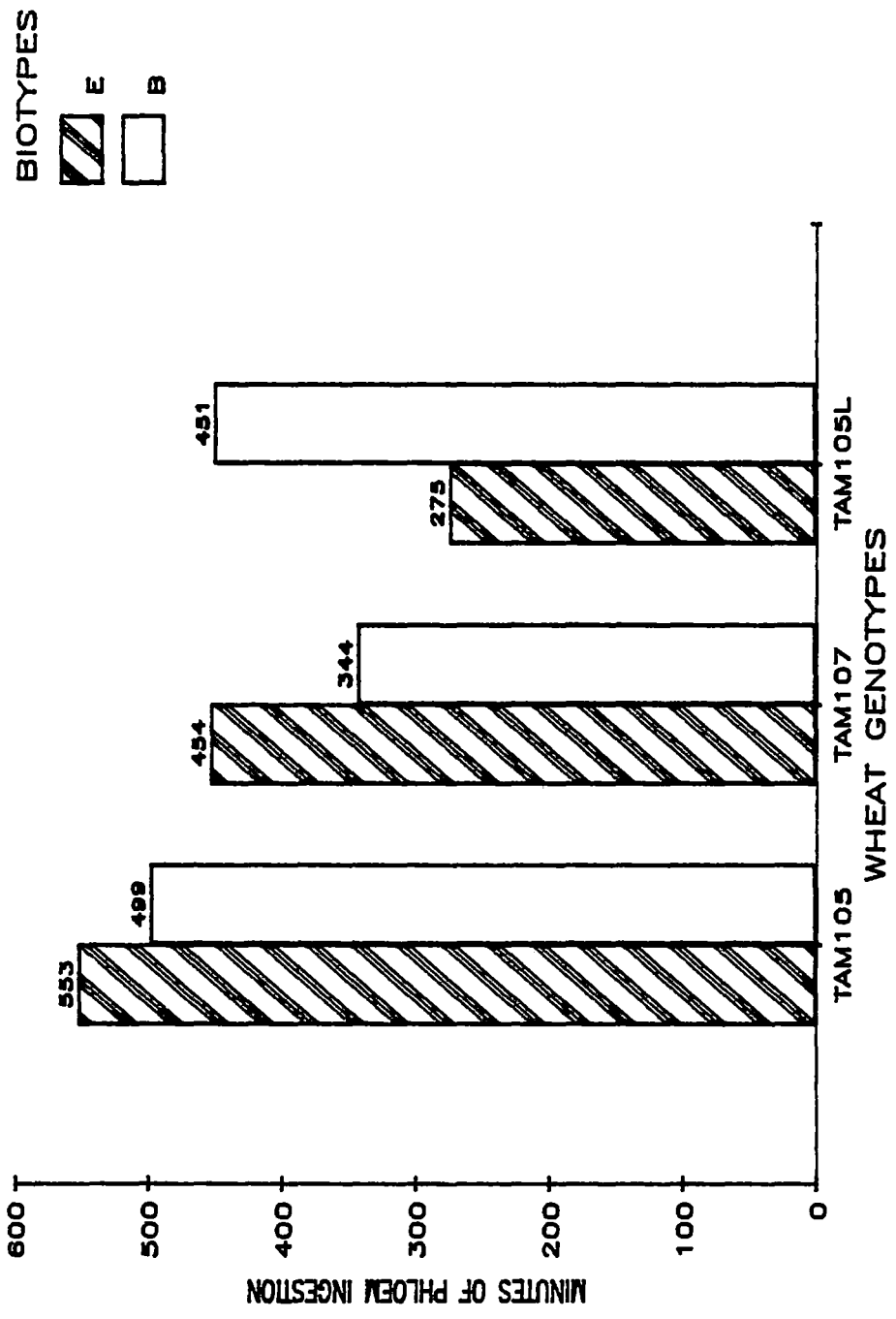

BIOTYPES
E
B
MINUTES OF PHLOEM INGESTION
600
500
400
300
200
100
0
553
499
454
344
275
451
TAM105
TAM107
TAM105L
WHEAT GENOTYPES

Figure 7. Time (in minutes) it Takes for the Greenbug to Start Its Committed Phloem Ingestion (lasting more than 15 minutes) as Observed During 720 Minutes of Monitoring Biotypes B and E Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105

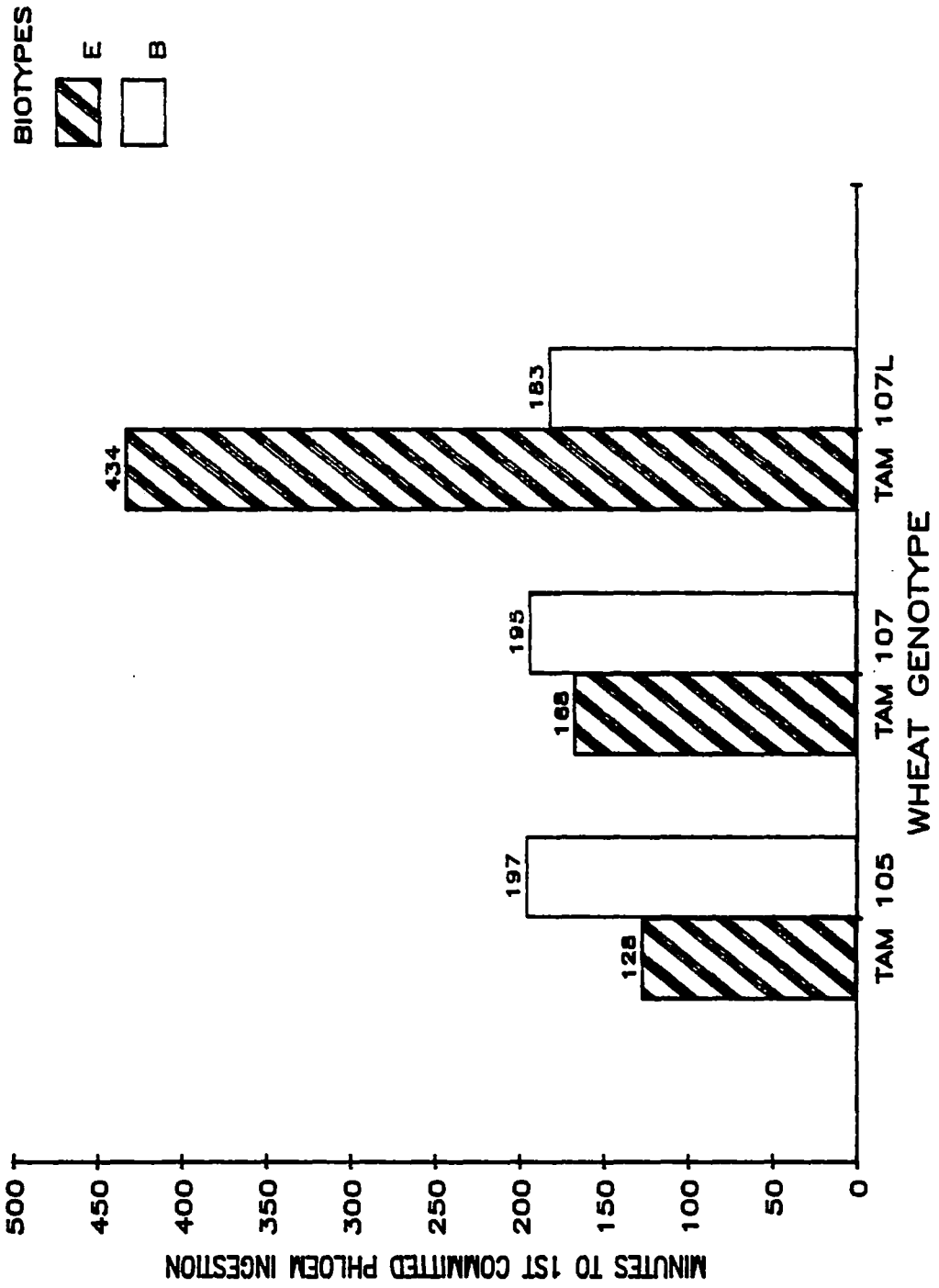

BIOTYPES
E
B
MINUTES TO 1ST COMMITTED PHLOEM INGESTION
500
450
400
350
300
250
200
150
100
50
0
128
197
168
195
434
183
TAM 105
TAM 107
TAM 107L
WHEAT GENOTYPE

TABLE IV

FEEDING BEHAVIOR PER FOUR HOUR INTERVALS OF MONITORING GREENBUG BIOTYPES B AND E ON THREE WHEAT GENOTYPES

Genotype/ Biotype	Monitoring Hours	TIME IN MINUTES						FREQUENCY	
		Baseline	Probing	Salivation	X-Waves	Phloem Ingestion	Non-Phl. Ingestion	X No. X-Wave	X No. Probe
TAM 105	0-4	14.5	2.5	88	1.4	117	16.5	2.1	5.9
Biotype E	4-8	1.1	0.3	11	0.2	227	0.6	1.1	1.5
	8-12	0.3	0.1	17	0.4	209	12.3	1.1	1.3
Total Time		15.9	2.9	116	2.0	553	29.4		
TAM 105	0-4	13.3	2.4	133	2.2	76	12.7	3.4	6.8
Biotype B	4-8	1.7	0.1	36	0.8	201	0.0	1.8	1.3
	8-12	0.2	0.1	18	0.5	221	0.0	1.5	1.0
Total Time		15.2	2.6	187	3.5	498	12.7		
TAM 107	0-4	11.3	1.8	82	0.9	96	47.6	1.5	4.8
Biotype E	4-8	9.4	0.6	36	0.4	176	17.0	1.4	3.0
	8-12	4.4	0.6	46	0.4	182	6.3	1.5	2.1
Total Time		25.1	3.0	164	1.7	454	70.9		
TAM 107	0-4	5.3	1.8	95	1.9	84	51.7	3.4	4.8
Biotype B	4-8	10.5	1.8	87	0.8	134	6.0	1.6	4.5
	8-12	10.2	2.0	92	0.9	126	8.6	1.9	6.8
Total Time		26.0	5.6	274	3.6	344	66.3		
Largo X TAM 105	0-4	30.2	3.3	68	0.5	25	113.2	1.3	9.9
Biotype E	4-8	13.5	1.2	96	1.6	90	37.1	3.0	4.5
	8-12	23.1	0.6	46	1.0	114	55.2	1.9	1.9
Total Time		66.8	5.1	210	3.1	229	205.2		
Largo x TAM 105	0-4	10.4	3.2	112	1.7	92	20.5	2.8	6.9
Biotype B	4-8	3.7	1.1	61	1.6	171	1.6	2.8	3.3
	8-12	2.6	0.6	48	0.9	185	2.4	2.0	2.4
Total Time		16.6	4.9	221	4.2	448	24.5		

ingestion with greatly reduced time spent in baseline, salivation and non-phloem ingestion. On Largo x TAM 105, there was increased phloem ingestion but not up to half of the total time. The broken resistance showed a decrease in baseline duration time and non-phloem ingestion, but increased phloem ingestion compared to the resistant.

b. Biotype B. In the first four hours, there was slightly more salivation duration, but shorter phloem ingestion on TAM 105 compared to the resistant TAM 107 or Largo x TAM 105 (Table IV). The phloem ingestion of biotype B on TAM 105 was much less than that of E on the same genotype.

During the next four hours, the baseline duration, the number of probes, salivation duration and non-phloem ingestion duration dropped while phloem ingestion was increasing on TAM 105 as compared to TAM 107. In the broken resistance, Largo x TAM 105, the baseline, salivation, and non-phloem ingestion durations were nearly twice as great as those in TAM 105.

By the third four-hour period biotype B continued phloem ingestion for virtually the entire time on TAM 105 whereas all other events were greatly reduced. Phloem ingestion remained at about half the activity time in the resistant TAM 107, but in the broken resistance of Largo x TAM 105, phloem ingestion time was showing a slight increase to about three-fourth of the activity time.

B. Survival

1. Growth

There were over twice as many greenbugs of each biotype produced on the susceptible as on the resistant genotypes for the respective biotypes

(Table V, Fig. 8). The broken resistances were intermediate, but were more similar to the susceptibles.

Biotype E greenbugs weighed significantly ($P \leq 0.05$) more (live weight) on the susceptible than on the resistant genotypes. It also produced heavier offspring compared to B on each genotype. There was no statistically significant difference ($P < 0.05$) in live weight per insect in the case of biotype B on the respective genotypes (Table V, Fig. 9). The live weight represented the total biomass of nymphs which became adults during the period as well as new nymphs produced. Based on the live weight per greenbug, biotype E performed better than biotype B. Biotype B on TAM 105 was not heavier on a live weight per greenbug basis, than on the other two genotypes. I included dry weight information in case there were differences in water content and did observe possible trends but interactions of biotypes by genotypes were also significant for all measurements other than live weight per greenbug.

2. Honeydew production

Honeydew production (Table VI, Fig. 10) was relatively complex since it might indicate both food availability and the aphid's ability to utilize plant sap for a nutritionally adequate diet. The analysis indicated a significant interaction ($P \leq 0.05$) for variety by biotypes, but such significance ($P = 0.245$) was not seen when I looked at honeydew production per greenbug (Fig. 11). The differing number of insects produced on the susceptible, resistant, and broken resistant genotypes constitute one factor considered. The honeydew per greenbug and per unit of dry weight was included to explain biomass gain in relation to excretion (honeydew) since the material removed from the host was weighed

TABLE V

MEAN GREENBUG NUMBERS, LIVE WEIGHTS, DRY WEIGHTS, AND LIVE WEIGHT PER INSECT (WEIGHTS ARE IN MILLIGRAMS) OF GREENBUG BIOTYPE B AND E FED ON THREE WHEAT GENOTYPES FOR 10 DAYS

Wheat Genotype	Greenbug Biotype	Mean No. Greenbugs	Live Weight (mg)	Live Weight per Greenbug (mg)	Dry Weight (mg)
TAM 105	E	153a[1]	26.5a	0.176a	7.9a
TAM 105	B	136a	17.8b	0.122bc	5.9a
TAM 107	E	129a	18.3b	0.139b	6.1a
TAM 107	B	56b	4.9c	0.088c	2.0b
Largo x TAM 105	E	69b	7.8c	0.115c	3.0b
Largo x TAM 105	B	152a	16.7b	0.112bc	5.9a
TAM 105	Both	144x	21.6x	0.149x	6.8x
TAM 107	Both	93y	11.6y	0.114y	4.0y
Largo x TAM 105	Both	110y	12.3y	0.114y	4.4y
All	E	117e	17.5e	0.143e	5.7e
All	B	115e	12.8f	0.107f	4.5e

[1] Values in each column with the same letters are not significantly different ($P < 0.05$). Comparisons were restricted to biotype/genotype combinations, or genotypes and biotypes within each column.

Figure 8. Mean Greenbug Biotypes B and E Numbers Produced During 10 Days of Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105

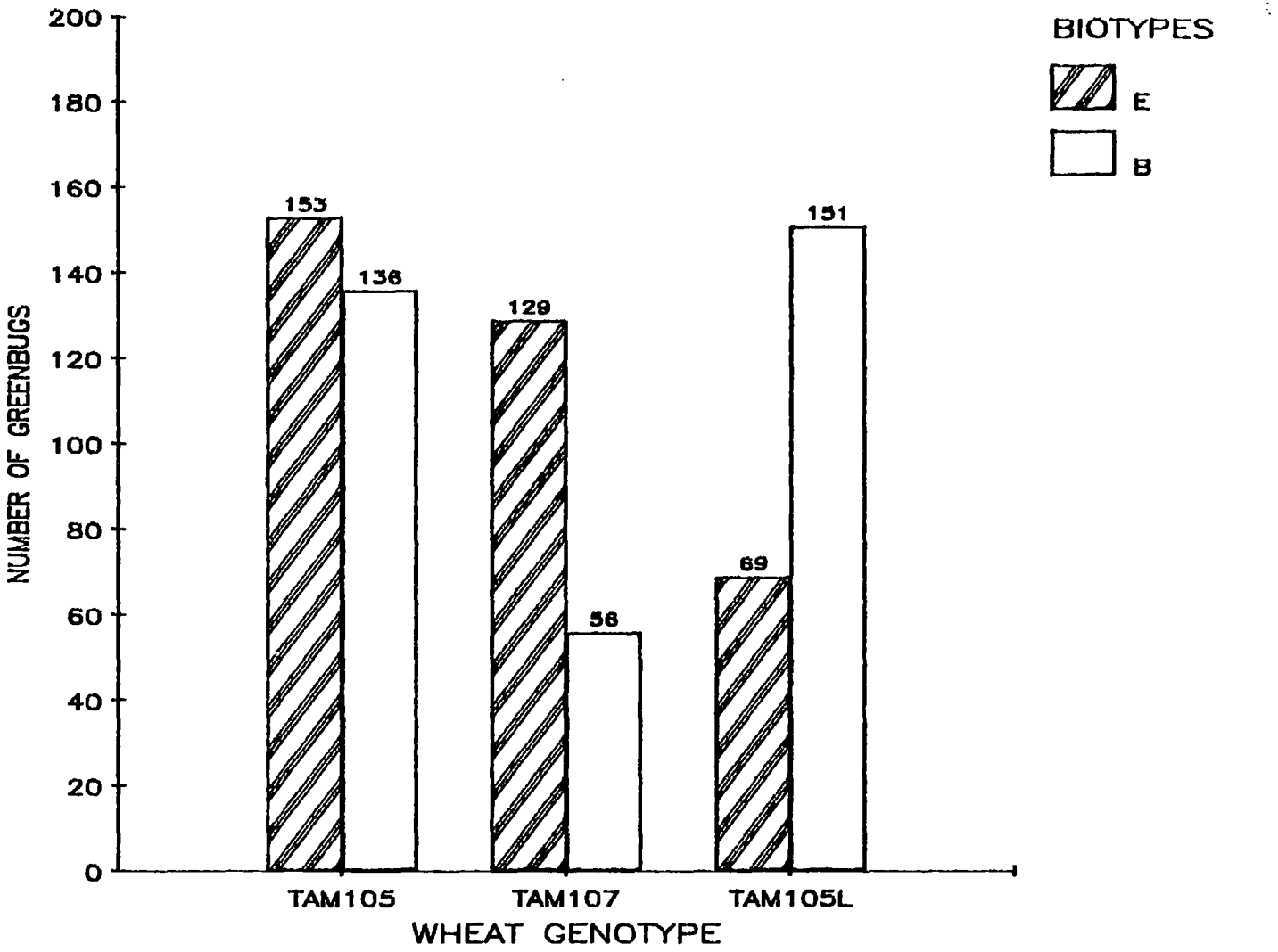

BIOTYPES
E
B
NUMBER OF GREENBUGS
200
180
160
140
120
100
80
60
40
20
0
153
136
129
56
69
151
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

Figure 9. Average Live Weight (in milligrams) per Greenbug of Biotype B and E Feed on Three Wheat Genotypes for 10 Days
TAM 105L = Largo x TAM 105

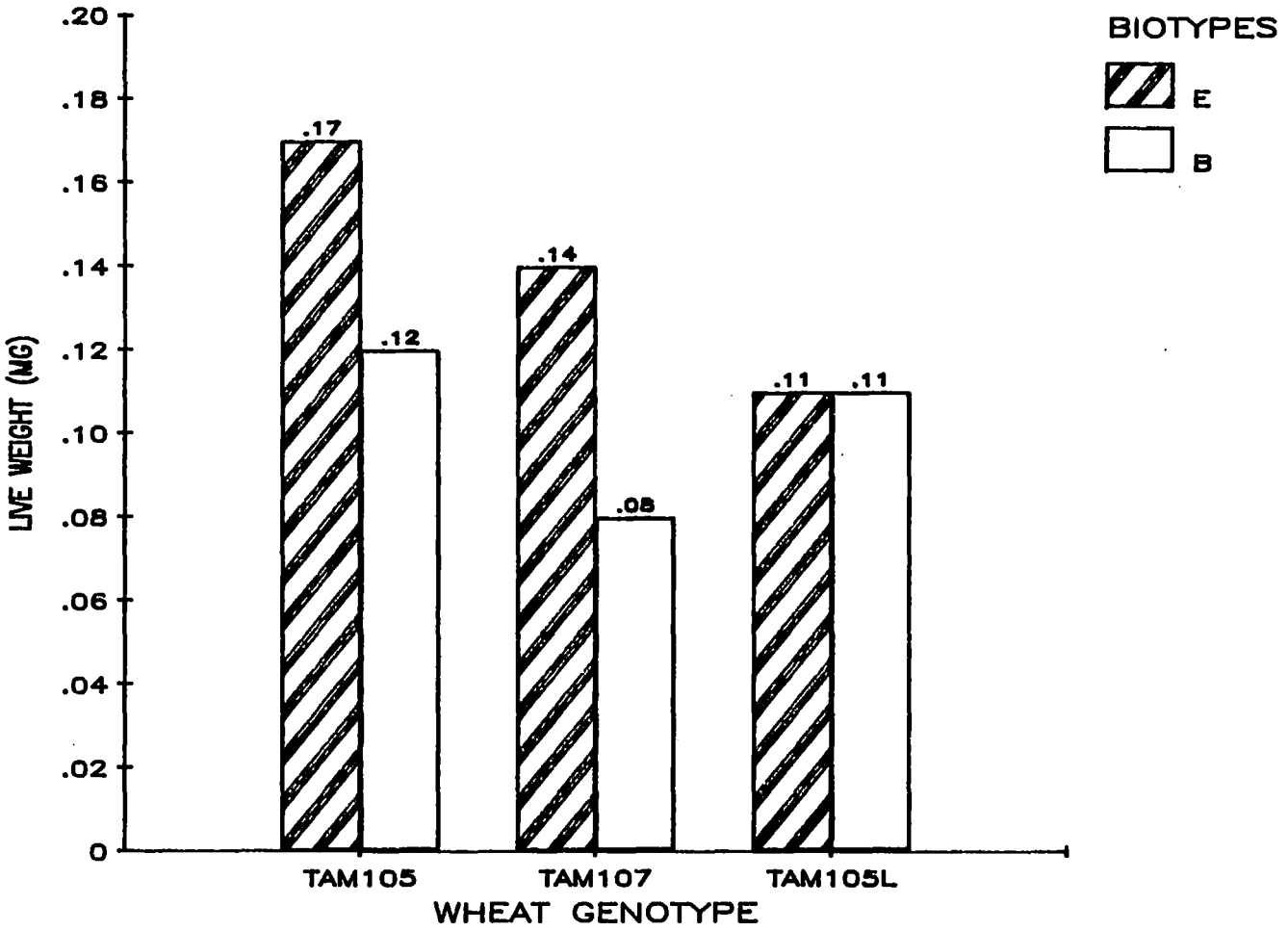

.20
.18
.16
.14
.12
.10
.08
.06
.04
.02
0
LIVE WEIGHT (MG)
.17
.12
.14
.08
.11
.11
TAM105
TAM107
TAM105L
WHEAT GENOTYPE
BIOTYPES
E
B

TABLE VI

MEAN GREENBUG NUMBERS, TOTAL HONEYDEW, HONEYDEW PER GREENBUG, AND HONEYDEW PER GREENBUG PER DRY WEIGHT (HD/GB/DW) PRODUCED BY BIOTYPE B AND E FEEDING ON THREE WHEAT GENOTYPES FOR 10 DAYS

Wheat Genotype	Greenbug Biotype	No. of Greenbugs per Replication	Honeydew Weight (mg)	Honeydew per Greenbug (mg)	HD/GB/DW
TAM 105	E	153a[1]	11.3a	0.057bc	1.44bc
TAM 105	B	136a	6.8bc	0.050c	1.21c
TAM 107	E	129a	10.6a	0.082ab	1.75abc
TAM 107	B	56b	4.5c	0.074bc	2.12ab
Largo x TAM 105	E	69b	7.0bc	0.104a	2.42a
Largo x TAM 105	B	152a	8.9ab	0.065bc	1.66bc
TAM 105	Both	144x	9.1x	0.062x	1.33x
TAM 107	Both	93x	7.6x	0.078xy	1.94y
Largo x TAM 105	Both	110y	8.0x	0.084y	2.04y
All	E	117e	9.7e	0.087e	1.87e
All	B	115e	6.8f	0.063f	1.66e

[1] Values in each column with the same letter are statistically similar ($P < 0.05$). Comparisons were restricted to biotype/genotype combinations, or genotypes and biotypes within each column.

Figure 10. Total Honeydew Produced (in milligrams) by Greenbug Biotypes B and E Fed on Three Wheat Genotypes for 10 Days
TAM 105L = Largo x TAM 105

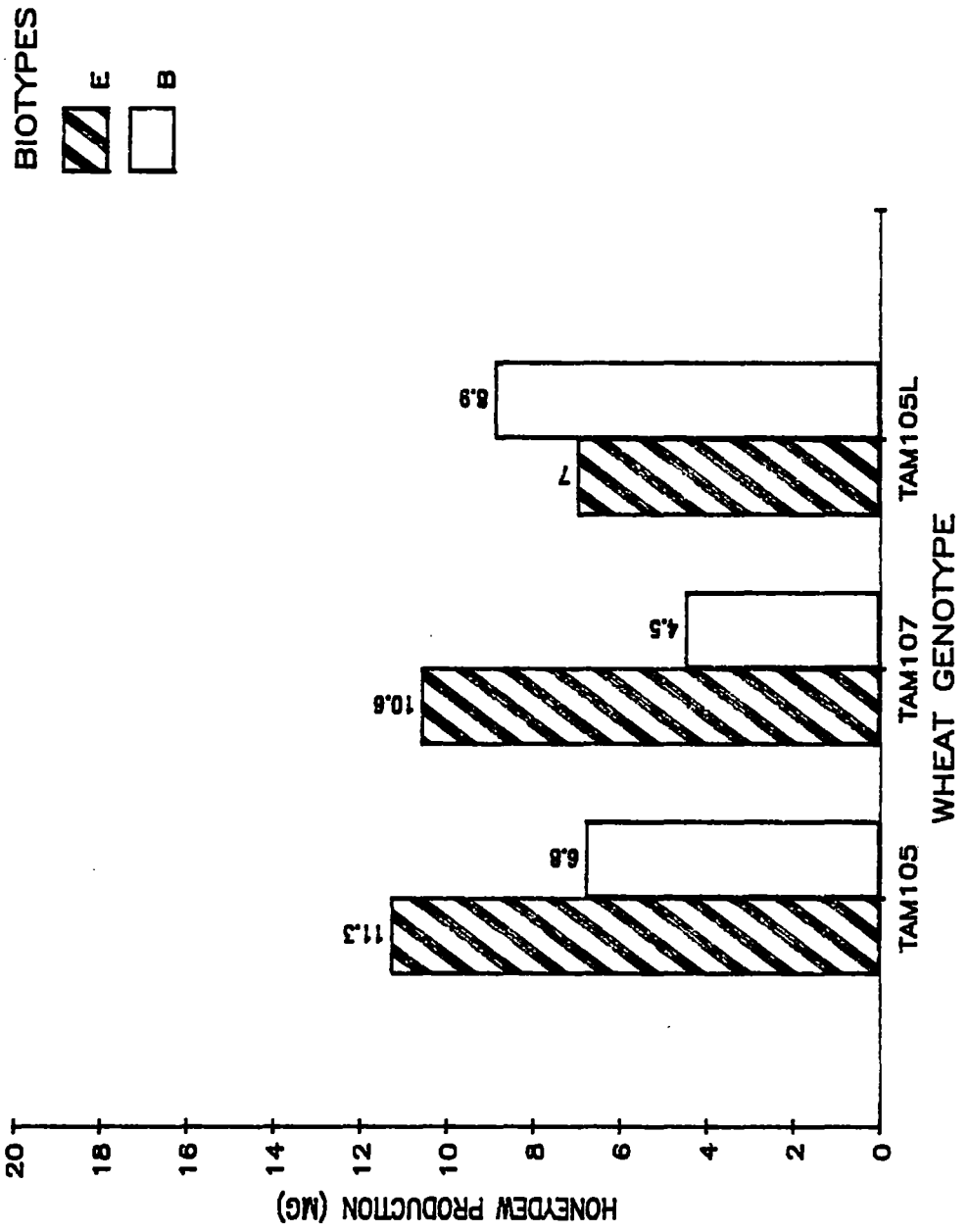
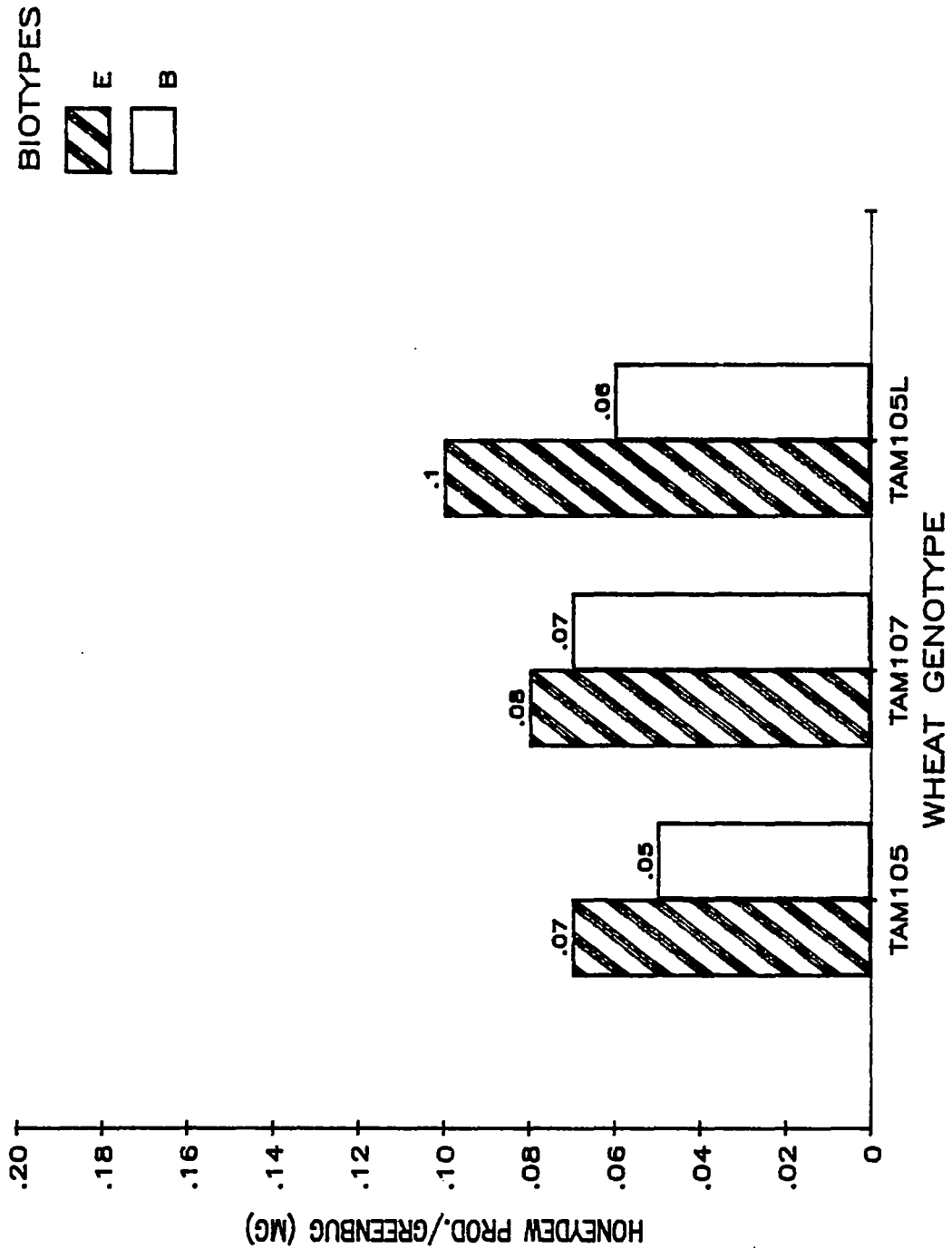

BIOTYPES
E
B
HONEYDEW PRODUCTION (MG)
0
2
4
6
8
10
12
14
16
18
20
11.3
6.8
10.6
4.5
7
8.9
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

Figure 11. Average Honeydew Produced (in milligrams) per Greenbug Biotypes B and E Fed on Three Wheat Genotypes for 10 Days TAML = Largo x TAM 105


BIOTYPES
E
B
HONEYDEW PROD./GREENBUG (MG)
.20
.18
.16
.14
.12
.10
.08
.06
.04
.02
0
.07
.05
.08
.07
.1
.06
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

as dry weight of greenbug or honeydew or escaped as water vapor (which was not accounted for).

Biotype E produced more honeydew per greenbug than biotype B (Table VI, Fig. 11). The effects of genotypes on biotype B were not significant when honeydew per insect was considered, but, when adjusted for dry weight, significantly ($P \leq 0.05$) more honeydew was produced on the resistant TAM 107 than on the susceptible TAM 105 (Table VI, Fig. 12). Biotype E also showed significantly ($P \leq 0.05$) more honeydew per greenbug, and honeydew per greenbug unit dry weight on the resistant than on the susceptible. In both honeydew per greenbug and honeydew per greenbug per unit dry weight, broken resistances were intermediate.

C. Damage

In all genotypes, there was a significant ($P \leq 0.05$) reduction in chlorophyll as compared to the respective checks. There was significantly ($P \leq 0.05$) less chlorophyll reduction in resistant combinations compared to the susceptible (Table VII, Fig. 13). The broken resistance to E was intermediate, whereas the broken resistance to B was similar to the susceptible. The percent reduction column and Figure 14 were included to help visualize the relative responses.

Figure 12. Average Honeydew Produced Per Greenbug and Per Unit Dry Weight for 10 Days of Feeding on Three Wheat Genotypes. TAM 105L = Largo x TAM 105

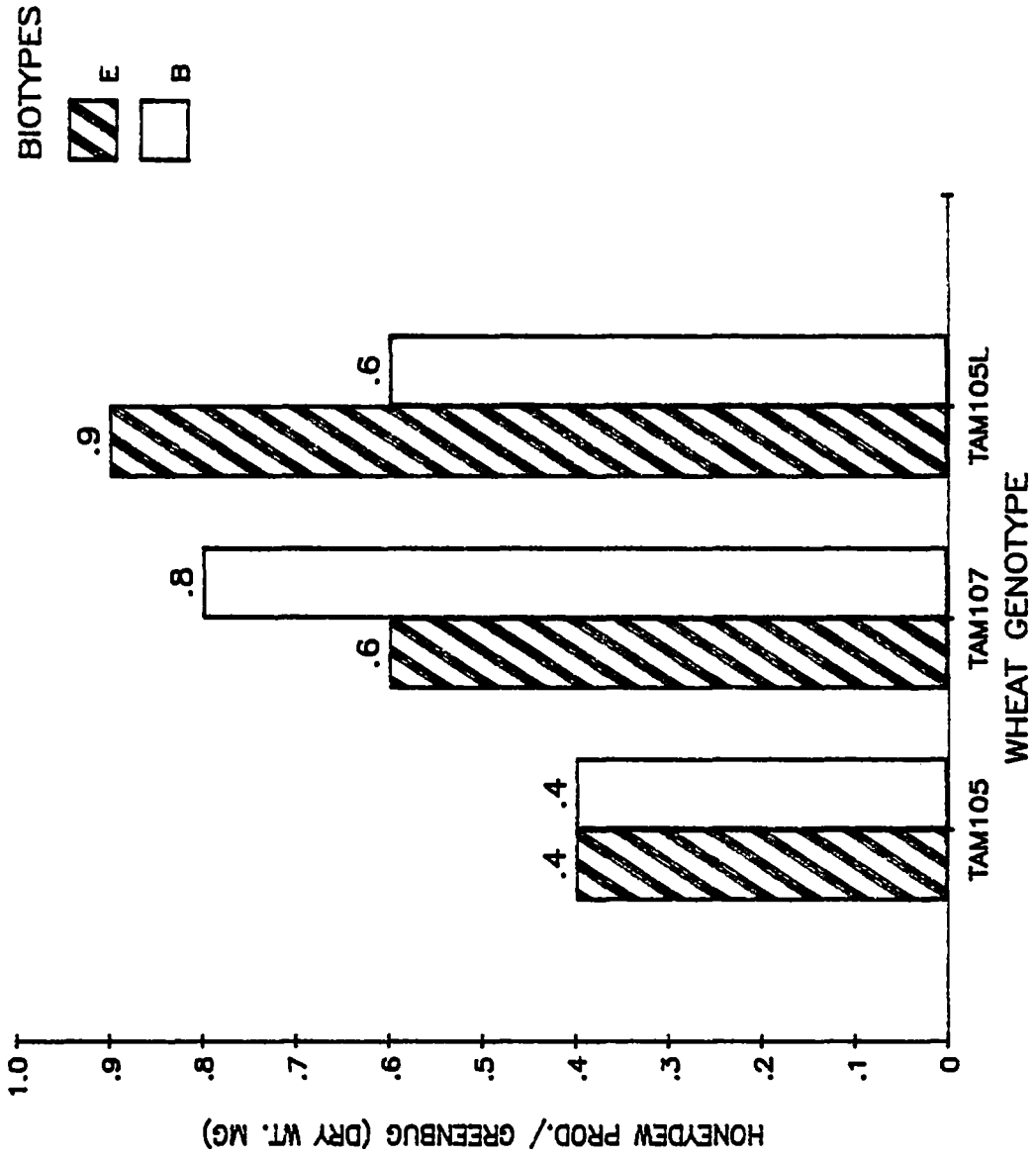

BIOTYPES
E
B
HONEYDEW PROD./ GREENBUG (DRY WT. MG)
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
.4
.4
.6
.8
.9
.6
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

TABLE VII

TOTAL CHLOROPHYLL MEASUREMENTS (MG/G OF FRESH WEIGHT) OF INFESTED AND UNINFESTED LEAVES, AND PERCENT CHLOROPHYLL REDUCTION DUE TO BIOTYPES B AND E FEEDING ON THREE WHEAT GENOTYPES

Wheat Genotype	Greenbug Biotype	Chlorophyll (mg) Infested	Chlorophyll (mg) Uninfested	Percent Reduction
TAM 105	E	661d[1]	1626ab[1]	59%
TAM 105	B	536d	1626ab	67%
TAM 107	E	857cd	1673ab	49%
TAM 107	B	1316b	1673ab	21%
Largo x TAM 105	E	1297bc	1824a	29%
Largo x TAM 105	B	571d	1824a	69%

[1] Values with the same letters in both chlorophyll columns are not significantly different ($P < 0.05$).

Figure 13. Total Leaf Chlorophyll Content (in mg/g of leaf per weight) of Three Wheat Genotypes Before (check uninfested) and After 10 Days of Greenbugs Biotype B and E Feeding
TAM 105L = Largo x TAM 105

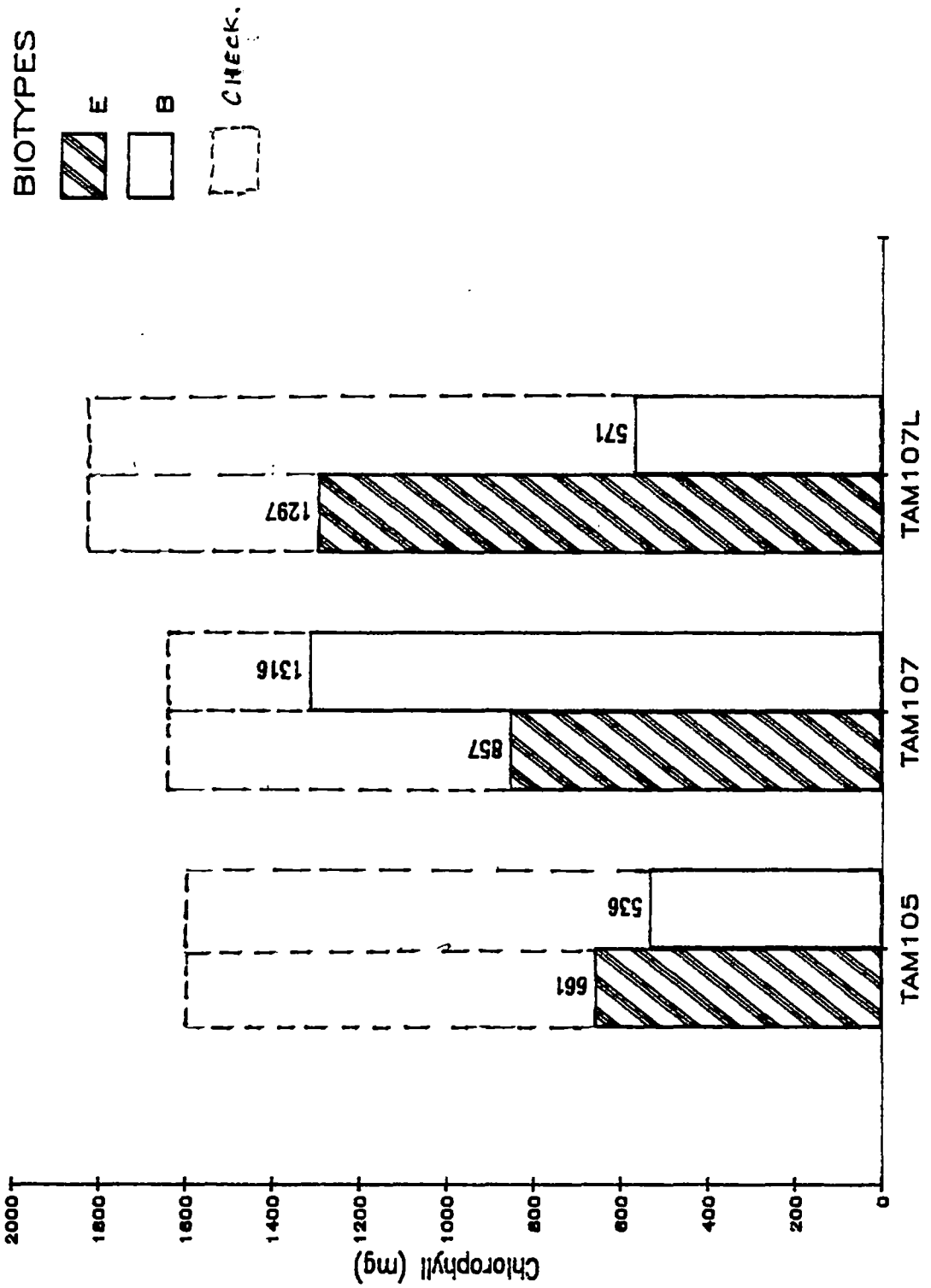
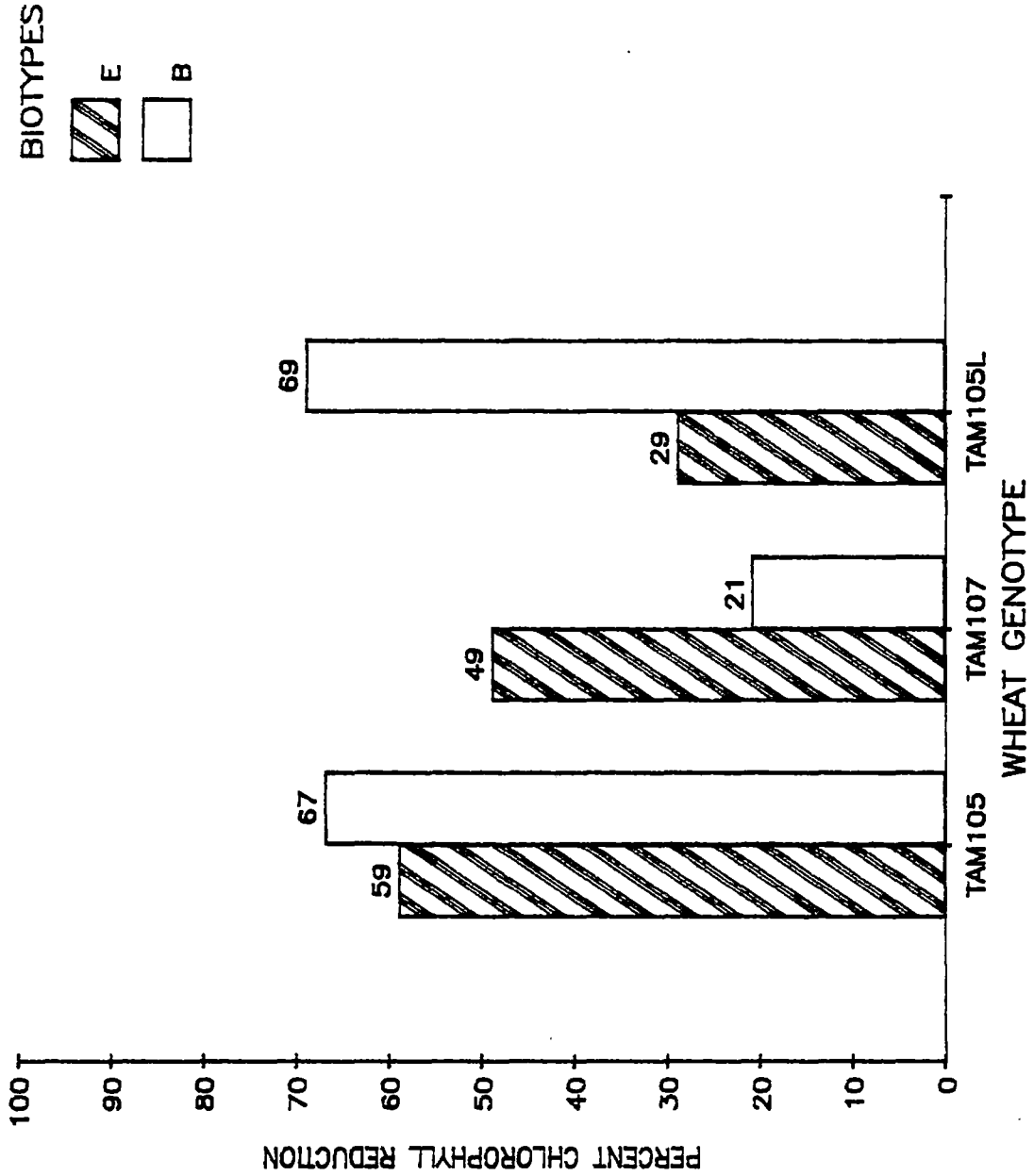

BIOTYPES
E
B
CHECK.
Chlorophyll (mg)
0
200
400
600
800
1000
1200
1400
1600
1800
2000
TAM105
661
536
TAM107
857
1316
TAM107L
1297
571

Figure 14. Percent Chlorophyll Reduction Due to Greenbug Biotypes B and E Feeding on Three Wheat Genotypes for 10 Days TAM 105L = Largo x TAM 105


BIOTYPES
E
B
PERCENT CHLOROPHYLL REDUCTION
100
90
80
70
60
50
40
30
20
10
0
59
67
49
21
29
69
TAM105
TAM107
TAM105L
WHEAT GENOTYPE

CHAPTER IV

DISCUSSION

In three of the feeding behavior events (probes, salivation and phloem ingestion), there were significant differences between resistant and susceptible wheat genotypes to the respective greenbug biotypes. In addition, biotype E showed significant differences in baseline, probes, X-waves, time to first x-wave, and time to first committed phloem ingestion.

McLean and Kinsey (1968) found significant differences between aphid feeding on host and nonhost plants. In my experiments the resistant plants could be considered as nonhosts and the susceptible plants as hosts; thus the difference observed in aphid feeding behavior between resistant and susceptible could be viewed as nonhost versus host relationship. As expected, the feeding behavior studies showed that greenbugs fed less successfully on resistant plants as indicated by reduced phloem ingestion, but increased inactivity duration (baseline), higher frequencies of epidermal penetration (probes) and phloem penetration (x-waves). Moreover, the relatively short salivation duration on the susceptible genotype TAM 105 compared to the resistant genotypes pinpoints the difficulties the greenbugs had when feeding on the resistant wheats.

Ryan et al. (1986) found similar results on 'Largo' compared to another susceptible wheat variety, 'Sturdy'. There was less feeding

behavior success by biotype E on the resistant 'Largo' wheat compared to the susceptible 'Sturdy'. The 'Largo' gene present in the Largo x TAM 105 has conferred high resistance in this genotype as indicated by the results. As a matter of fact, the differences between the susceptible and resistant genotypes to biotype E were consistant in all the feeding behavior events. It is likely that resistance to biotype E is more effective than resistance to biotype B. This indicates a possible difference in the mechanisms of resistance involved in these two sources. As indicated earlier, the resistance to B that exists in TAM 107 is conferred by the 'Amigo' gene. This resistance was more variable than that in Largo x TAM 105 when feeding behavior was considered. Biotype B salivated more than biotype E in all wheat genotypes; this is probably a difference between the two biotypes.

Ryan et al., (1986) stated that ultimately greenbugs feed in the phloem (the feeding site), but that the differences due to host could be seen in the early hours after the greenbug contacts the host. Thus, a resistant plant most likely delays aphid feeding on the host, and consequently would delay damage. I have found that the greenbug feeding behavior changed through time depending on the host. In all genotypes, the greenbugs were showing a significant and progressive increase in phloem ingestion through time while they expended less time in probing, salivation and attempting to penetrate the phloem.

Because of many unusual patterns in biotype E/Largo x TAM 105 combination, additional aphids were monitored on this host in an attempt to obtain comparable results. When the host is acceptable to the insect, the feeding pattern follows the regular sequence described earlier. The deviations I saw in this combination could be an indication that the host

was very unsuitable to the greenbug, to the extent that it could not feed properly. The resistance in 'Largo' is highly effective to biotype E. I found that the overall trend in feeding behavior over time was the same and that there was an increase in phloem ingestion regardless of the host and biotype. These results confirm those by Ryan and coworkers.

McLean and Kinsey (1968) found that 70% of the pea aphids made the same amount of probes during the first minutes of contact with the host, and non-host but differences due to host occurred later. Even though these two workers did not use the greenbug, I saw the similarity of their results to mine. Biotype E probed more on Largo x TAM 105 plants than it did on any other combination or than B did. The resistance of 'Largo' containing wheat to biotype E could be seen in less than 240 minutes following contact but also persisted in causing less phloem ingestion during the next 480 minutes.

The broken resistances to respective biotypes were variable. In probe frequencies all broken resistances were similar to the susceptible TAM 105. However, in phloem ingestion and salivation, the broken resistances to respective biotypes were similar to the respective resistant genotypes. In other behavior characteristics, they were intermediate or susceptible. These results were not totally in conformation with my expectations on the broken resistances. They were expected to react similar to the susceptible TAM 105, but apparently the broken resistances are not always susceptible, they may still have some level of resistance.

Greenbugs reproduced less on resistant plants and individuals produced on such plants were smaller despite the increased honeydew uptake. There were fewer insects of biotype E on the 'Largo' containing

genotype and fewer of B on the 'Amigo' containing genotype. The amount of honeydew produced per insect of biotype E on the resistant is higher than that on the susceptible. Greenbugs ingest fluid extracted from the plant. If the fluid is of good nutritional quality, more may be assimilated into biomass and thus less would be excreted as waste (honeydew). If the fluid is poor in nutritional value, less of it would be assimilated into biomass, thus more would be excreted as honeydew. I think that since greenbugs were smaller and excreted more honeydew on the resistant plants, there may be a poorer nutritional value of the extracted fluid making it less assimilable by the insect. This explains what was observed on Largo x TAM 105 plants. The difference was not seen in any other combination. Starks et al. (1983) found that the 'Largo' gene mediated high antibiosis, tolerance and even antixenosis mechanisms of resistance against biotype E. My results confirm the antixenosis and antibiosis mechanisms. Biotype E weighed less but consumed (or excreted) more fluid per unit of weight when honeydew per insect and per unit dry weight was measured. As mentioned earlier, each insect excreted more honeydew, possibly because of the poor quality of the sap ingested and consequently poor assimilation and reduced weight. These may be signs of antibiotic effects. The reduced reproduction (fewer insects) could then be another explanation of the antibiotic mechanism. There may be some chemical present in the plant sap making it less digestable to the greenbug, but this needs further investigations.

There were no statistical differences in total honeydew production and honeydew produced per greenbug between resistant and susceptible genotypes to biotype B. The fewer nymphs produced on TAM 107 suggested that there may be antibiosis. Starks et al. (1983) indicated that the

'Amigo' gene conferred non-preference against biotype E rather than antibiosis. Under my experimental conditions, the results have shown that 'Amigo' gene could impart antibiosis. Results from the growth and honeydew studies have supported the point Starks et al. (1983) made on 'Largo' but showed that 'Amigo' gene also confers antibiosis to the TAM 107 genotype. The feeding behavior studies which were essentially host preference studies indicated that the 'Largo' containing genotype was not preferred by biotype E and the 'Amigo' containing one not preferred by biotype B. Furthermore, I was able to see that when broken resistances were used, the results varied from resistance to susceptibility and that in all feeding behavior events, resistance in Largo x TAM 105 was always apparent. The honeydew and growth studies indicated that even though fewer aphids were produced on the TAM 107, resistant to biotype B, the effect of the nutritional quality was apparent in that less honeydew was produced per mg dry weight by biotype B on TAM 105 than on TAM 107.

My results were comparable to those of Gerloff and Ortman (1971), since despite the fact that there was reduction of chlorophyll in all genotypes, more chlorophyll was lost in the susceptibles. The B combinations caused a relatively greater loss of chlorophyll. As mentioned in earlier chapters the cause of damage was generally thought to be the saliva and food uptake. The damage to leaves was mainly due to saliva as Chatters and Schlehuber (1951), and Al-Mousawi et al. (1983) had pointed out. The latter have postulated that the toxic saliva may be dissipated or adsorbed by resistant tissues, thus become nontoxic. This may be what happened in our resistant entries. However, the amount of the salivary toxic activity which could be buffered by the resistant plant is unknown, but it is certain that not all of it can be buffered

since chlorophyll reduction was observed in all combinations. Probably, the more saliva that could be broken down, the less chlorophyll reduction occurred. The toxic factors of the saliva and the factors that could cause detoxification of the saliva in the resistant plant are unknown. Pennington (1985) noted that phenolic compounds and silicon were abundant around the aphid feeding area. These phenolic compounds may contribute to detoxification of saliva in barley. Corcuera et al. (1982) mentioned hydroxamic acid as a feeding deterrent to greenbug in wheat. Chemicals might be involved in salivary adsorption in these resistant wheat genotypes, but no experiment was designed for such studies.

Reduction in chlorophyll due to biotype E on its resistant Largo x TAM 105 was similar to that due to B on its resistant TAM 107 (Amigo x TAM 105). In other words, in terms of affecting the degree of damage, the 'Amigo' gene does not differ from the 'Largo' gene. Thus if 'Largo' gene confers tolerance to biotype E, then 'Amigo' gene would also confer tolerance due to similarity in chlorophyll reduction. Furthermore, since chlorophyll reduction in the resistant combination was as low as 20 to 30%, I infer that tolerance may be involved, but insect numbers were not the same for each genotype as they should be in tests for tolerance.

The broken resistances to both insects showed damage similar to susceptibles, but reduction in chlorophyll by biotype B in Largo x TAM 105 was even higher than that in the susceptible TAM 105. This shows that biotype B is definitely virulent to the 'Largo' gene, and these results conform to Webster et al. (1986). As a matter of fact, the observed reduction in chlorophyll was as high as 69% when biotype B fed on Largo x TAM 105.

To briefly review what was observed, I can say that on the

To briefly review what was observed, I can say that on the susceptible genotype to both biotypes, there was less salivation duration, but more chlorophyll removal compared to the respective resistant genotypes. The broken resistance to E was intermediate in both salivation duration and chlorophyll removal whereas the broken resistance to B was like a susceptible. Thus, susceptible combinations showed more damage than resistant ones because of higher greenbug populations. Broken resistance to E was intermediate as far as damage versus greenbug numbers was considered, but broken resistance to B was not.

The least total honeydew per greenbug and per greenbug dry weight was produced on the susceptibles. In other words, less honeydew per greenbug was produced where there was more damage. Thus the lower the amount of honeydew produced, the more efficiently the insects feed, and consequently the higher the damage observed. Therefore, I had more chlorophyll removal when the greenbug fed, and survived successfully on a host. Overall, biotype B produced less honeydew, indicating that this biotype is probably more efficient in using these wheat genotypes for food than the biotype E.

CHAPTER VI

SUMMARY AND CONCLUSIONS

From these studies, I have been able to note that there are variations in feeding behavior of the greenbug biotypes B and E on the three wheat genotypes. Those variations may be due to the aphid themselves (difference in biotype virulence) or to the host. The greenbugs feed less successfully on resistant plants, and the 'Largo' gene was apparently a highly resistant gene compared to the 'Amigo' gene. It was found that biotype B salivated and made more x-waves on all wheat genotypes than E did. I cannot explain these observations as such, but I may speculate that these are variations in the biotypes themselves. The broken resistances caused varied responses from the biotypes. Given all these results, I can say that non-preference is involved in both resistant genotypes.

The survival studies have indicated a strong possibility for antibiosis in the 'Largo' containing genotype to biotype E, and for 'Amigo' containing genotype for biotype B. Further research on the chemical factor(s) causing the observed harmful effects on greenbugs feeding on 'Largo' and 'Amigo' seem desirable. The broken resistances gave variable responses as far as survival studies were concerned.

Finally, the damage due to greenbugs feeding on the leaves was characterized by the loss in chlorophyll. Resistant genotypes lost less chlorophyll than the susceptibles and the broken resistances were

variable in responses. Overall, resistance in Largo x TAM 105 to biotype E and that in TAM 107 to biotype B include antibiosis, antixenosis, and possibly tolerance. The variability in the broken resistance responses in feeding behavior, survival and damage, lead me to conclude that the resistance relationship is not a simple gene-to-gene response but may be controlled by more than one gene or a pleiotropic gene.

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